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STUDIES ON SOUTHEASTERN AQUATIC INSECTS

James B. Wallace

Georgia University

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This report is concerned with taxonomic studies of adult and immature Trichoptera in the southeast and several aspects of the ecology and distribution of southeastern aquatic insects. The distribution of the family Hydropsychidae in the Savannah River basin in relation to water quality parameters was studied. The effects of prolonged exposure to a chlorinated hydrocarbon insecticide, dieldrin, and its effect on aquatic insect populations and residue levels ~~is~~ are discussed. The feeding habits and feeding rates of an herbivorous stonefly were studied as well as the effect of such feeding on water quality--such as increased leaching from leaves as a result of insect feeding. In conjunction with the preceding laboratory experiments, an extensive study was carried out on the benthic fauna of four small streams of various plant cover types (Hardwood, Coppice Hardwood, White Pine and Pasture) in the southern Appalachians. The pine stream had lowest diversity and standing crop biomass, whereas the coppice had greatest standing crop biomass. Wholebody and standing crop of calcium, potassium and magnesium were also studied in the above streams. (EPA)

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STUDIES ON SOUTHEASTERN AQUATIC INSECTS

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ABSTRACT

This report is concerned with taxonomic studies of adult and immature Trichoptera in the southeast and several aspects of the ecology and distribution of southeastern aquatic insects.

The distribution of the family Hydropsychidae in the Savannah River basin in relation to water quality parameters was studied.

The effects of prolonged exposure to a chlorinated hydrocarbon insecticide, dieldrin, and its effect on aquatic insect populations and residue levels is discussed.

The feeding habits and feeding rates of an herbivorous stonefly were studied as well as the effect of such feeding on water quality; mainly through increased leaching from leaves as a result of insect feeding is discussed. In conjunction with the preceeding laboratory experiments, an extensive study was carried on the benthic fauna of four small streams of various plant cover types (Hardwood, Coppice Hardwood, White Pine and Pasture) in the southern Appalachians. The pine stream had lowest diversity and standing crop biomass, whereas the coppice had greatest standing crop biomass. Whole-body and standing crop of calcium, potassium and magnesium were also studied in the above streams.

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SECTION I

CONCLUSIONS

As a result of the taxonomic portions of this work, several facts have emerged: (1) the distribution of many species of Trichoptera in the southeast is much wider than originally supposed, (2) the region in general has been poorly collected since a number of new species are still being found, and (3) many factors such as available food supply, i.e., in the form of detritus, type of substrate, etc., appear to be just as important at times as water quality parameters in explaining the distribution of many species. In regard to the Hydropsychidae of the Savannah River Basin some species may have quite narrow tolerances in regard to temperature, dissolved oxygen, etc., and be quite limited in their distribution while other species even within the same genus may be quite widespread, occurring from the mountains to the coastal plain. Thirty-six species of Hydropsychidae were found in the Savannah River Basin alone.

The chlorinated hydrocarbon pesticide, dieldrin, had a profound influence in one area of the Savannah River Basin. Dieldrin in the effluent from a woolen mill greatly reduced downstream insect populations. Dieldrin residues in aquatic invertebrates upstream ranged from non-detectable to 0.69 ppm while residues up to 3 miles downstream, below the effluent, were as high as 100 ppm. Certain invertebrates were concentrating dieldrin up to 17,000 fold compared to water samples at the same location.

Laboratory studies revealed that the most abundant stonefly, Peltoperla, in the southern Appalachians consumed autumn shed leaves in amounts (by dry wt.) in excess of their dry body weight in a 2 week period. Herbivorous insects such as above form the basis for the major portion of the aquatic food in small and medium sized streams throughout the southeast. The finely ground leaf material in the feces of these herbivorous insects serve as food for fine particle feeders as well as resulting in increased leaching of certain leaf elements. In laboratory studies concentration of calcium, magnesium and sodium were significantly higher in containers where insects fed on the leaf material.

In extensive studies on four watersheds in the southern Appalachians (old field succession, hardwood forest, white pine forest, and coppice hardwood forest) the kinds of organisms in the four streams were relatively similar but their relative importance varied significantly. A Duncan's multiple-range test showed significant differences in the numbers of most taxa among watersheds. The old field succession stream had greatest diversity while the coppice hardwood stream had the greatest standing crop biomass. The white pine stream had lowest standing crops of both numbers and biomass. The white pine stream supported only 1/5 to about 1/2 as much animal biomass as the other four streams. In laboratory tests we found that pine needles were not a preferred food of an herbivorous stonefly naiad.

Ingestion rates calculated from literature values were in close agreement with the amount of available detritus (input) for consumption. This explains why there is no long-term accumulation of leaf detritus in streams.

Whole body and standing crops of calcium, potassium, and magnesium were studied on the above watersheds. Crayfish and salamanders account for most of the standing crop biomass in the detritivore and predator compartments, respectively, and these two organisms also account for most of the fluxes in their compartments. They may be especially important in stream nutrient flow, especially in the small soft water streams, by forming significant calcium sinks.

In general, potassium concentrations tend to increase with trophic level while calcium and magnesium decreased with increasing trophic level. Most detritivores concentrated proportionally more potassium than either calcium or magnesium.

SECTION II

RECOMMENDATIONS

Based on our distributional work of Hydropsychidae in the Savannah River Basin, establishment of any water quality parameters based on generic classification or a few species selected at random to serve as a basis for ecological planning and extrapolation for widespread regions of the country would appear to be of little value. To predict with any degree of certainty the ecological effects of man's varied activities upon the benthos of an area of stream, one should have a firm knowledge of the species composition of the fauna throughout that basin. For individual species this should include at least preferences in regard to stream size, temperature, dissolved oxygen, altitude, flow rate, substrate, food availability, and interactions with other species. Maximum summer temperatures of only a few degrees appear to be very important in limiting a number of Hydropsychidae genera and species. This is especially true of mountain and upper Piedmont species. Many environmental studies, involving benthos, have been hindered with only generic identifications with at most very few species.

In order to solve this problem it is necessary that considerable effort and emphasis must continue to be placed in adequate species characterization of immature stages where unknown. Also, continued support of association of immature stages should be encouraged along with extensive adult collecting. The genera of Trichoptera (and many other groups) can now be successfully identified in the immature stages for at least eastern North America. Efforts should be continued toward producing usable keys and biological information for individual species within these genera.

Studies should be initiated to develop techniques that would utilize specific invertebrates to be used as pesticide monitoring devices. If we have organisms that are concentrating pesticides several thousandfold above the amount present in the water, this will allow preliminary detection by relatively inexpensive gas chromatography equipment. The use of invertebrates also has several advantages over conventional techniques involving analysis of water samples alone.

These are as follows: (1) The bottom substrate with attached organisms would probably not be as susceptible to the continual flushing action of the stream as water samples, particularly grab samples. (2) The ability of certain aquatic invertebrates to concentrate pesticides several thousandfold over the concentration in the water would allow a pesticides detection, whereas conventional water analysis may indicate only a trace or no detectable amount of the pesticide at a particular time. (3) Since many invertebrates are relatively sessile, this would allow a technique that could help pinpoint a pesticide pollution source. Bottom organisms could possibly even aid in the detection of spots subjected to even periodic introduction of pesticides, whereas water samples alone, unless monitored constantly over a long period of time, might not detect such points of release.

It should be stressed that analysis of invertebrates would not replace conventional water analysis but augment it. Higher concentrations of pesticides in animals at a specific location would serve as a tool in locating point sources of pesticide pollution. Conventional water analysis could then be used to document if the area in question is currently active as a source of pesticide pollution.

The studies on the effect of plant cover types on stream benthos indicate that forest monoculture practices involving small pine watersheds may seriously affect secondary production of herbivorous aquatic invertebrates in small streams that rely largely on autumn shed leaves as a food source. Although not studied in this project one may surmise that channelization practices, in addition to disturbing the stream substrate, may also reduce secondary production of herbivorous aquatic invertebrates, especially those channelization practices that involve removal of vegetation surrounding streams. This aspect of channelization should certainly be tested for possible detrimental effects to the benthic fauna.

Extensive studies in the exact role of the microflora such as the aquatic fungi and bacteria in the leaf-insect relationship should be encouraged. Included in the above should be extensive studies on the fate of finely ground leaf material in the feces of herbivorous insects, especially in regard to fungi and bacteria and their possible utilization by downstream filter feeders. Much more effort needs to be devoted to this aspect of stream ecosystems.

SECTION III

GENERAL INTRODUCTION

The problem of systematics in stream ecology has become more evident than ever in recent years. H. B. N. Hynes (1970) reports that the ecology of stream insects is still largely exploratory and descriptive and we are beginning to understand some of the reasons for particular distributions in relation to substratum, temperature, seasonal cycles, etc. However, Hynes points out "we suffer greatly from our inability to identify immature insects." Usually it is the immature stage that stream ecologists encounter and identify to the best of their ability. Identification to genera, although often tenuous, is generally possible; however, species identification based on immature characters is generally impossible except in a few genera in specific regions of the country. One of the major goals of this study was to collect, rear, and describe immature stages of southeastern aquatic insects, particularly Trichoptera, and include information on their biology and water quality parameters.

Initial field work was devoted to: (1) extensive collecting of adults and larvae, utilizing light traps and sweep nets for adults and hand picking and dip nets for larvae, (2) determination of various water quality parameters at collection locations, and (3) laboratory rearing in order to associate immature and adult forms. Much of the effort was devoted to the Savannah River Basin in North Carolina, South Carolina, and Georgia. With headwaters arising in the mountains of western North and South Carolina and northern Georgia, this basin contains most of the major stream habitats found in the Appalachian, Piedmont and Coastal Plain Provinces of the southeast. A portion of the work on the Savannah River concentrated on the effects of dieldrin in the effluent of a woolen mill in South Carolina.

As the study developed it became evident that many things other than strict water quality parameters, such as substrate, available food, etc., play important roles in influencing distribution of many species of aquatic insects.

For example, many insects were almost invariably associated with leaf material in streams. Representatives of several orders fed readily on leaf material in the laboratory. This led to several studies involving consumption, preferences and possible effects of insects feeding resulting in increased leaching of leaves. An opportunity to study the importance, to stream organisms, of terrestrial litter input developed at the Coweeta Hydrologic Laboratory, U.S.D.A. (Forest Service) in western North Carolina, where a team of plant ecologists was studying terrestrial litter production as a part of National Science Foundation International Biological Program efforts. Monthly quantitative and qualitative samples were taken from each of four watersheds. Sampling, as systematics, is a major problem in stream ecology and as noted by Hynes (1970) most sampling tends to underestimate actual numbers and biomass. However, since all samples in the Coweeta watersheds were taken using the same instrument and identical sorting procedures, we can conclude that the degree of difference between the streams is reflected in the results.

Trophic activity of detritivores and their predators play important roles in the movement of nutrients during the leaf decomposition processes in these streams. Although gross energy budgets and food webs have been derived for many aquatic systems, there is very little published information on ingestion and egestion rates of individual aquatic insects. In many respects small woodland streams that have heavy terrestrial litter input are similar to adjacent soil litter systems, with different animals in the two systems performing similar roles. Investigations into the role of aquatic invertebrates in the distribution and transfer of elements found in leaf tissue during this decomposition process is lagging far behind that of soil litter systems. Some initial investigations into this area are being carried out in the Coweeta streams.

The body of this report consists of the following main areas of work:

(1) A review of taxonomic publications resulting from the project to date, and work and publications in progress.

(2) The distribution of the family Hydropsychidae in the Savannah River Basin.

(3) The effects of a dieldrin effluent on downstream populations of aquatic invertebrates and residual levels of dieldrin in certain groups.

(4) Selective feeding of an herbivorous stonefly on autumn shed leaf material.

(5) The influence of terrestrial vegetation and leaf material on the benthic fauna.

(6) Laboratory studies on leaching of leaves with insects feeding vs. insects excluded and

(7) Field studies on concentration and movement of selected elements in macroinvertebrates in small watersheds.

SECTION IV

TAXONOMIC STUDIES

Much of the time devoted to this project was devoted to taxonomic studies on southeastern Trichoptera. Several papers have already been published in scientific journals and are cited under publications in the back of this report; others are in progress.

Several new species have been described during the course of this project. They include one new species of *Psilotreta* (Trichoptera: Odontoceridae), three new species of *Lepidostoma* in the *vernalis* group from the southern Appalachians (this paper also included a revised key to males of all described species in the group). A new species of *Brachycentrus* was described in all stages, egg, larva, pupa, and adult, from Georgia. The larva of this species has two characters that do not agree with existing keys and larval diagnoses for *Brachycentrus* in the North American fauna; one of these features includes a larval case that is apparently unique for the entire family. The larval and pupal stages of *Anisocentropus pyraloides* (Trichoptera: Calamoceratidae) were also described along with data on their biology and water quality requirements. This presented the only account for the immature stages of this genus and species for North America. In another publication the larval stages of the 3 southeastern species of *Molanna* (Trichoptera: Molannidae) were described, along with information on their biology, feeding habits, water quality parameters and a key to species in the southeast. The larva of *Rhyacophila vuphiphes* Milne was also described. This was one of the few eastern *Rhyacophila* larvae that was unknown. It prefers medium sized rivers such as the Tallulah, Chattooga, Chauga, and Tugaloo in the Appalachian foothills.

One of the more significant taxonomic "finds" of this study was concerned with the identity of *Pseudogoera singularis* Carpenter. This species was originally described in 1933 (as new genus new species) on the basis of two males taken in the mountains of western North Carolina. No other adults have been reported since. It probably represented the last

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enigmatic genus of Trichoptera with uncertain affinities in eastern North America. A number of adults of this species were reared. The larvae appear to be fairly common at certain locations in the southern Appalachians and Appalachian foothills. They are found buried in moss growths on rocky areas or outcrops of streams. This genus had been placed in the family Goeridae of the limnephilid line on the basis of the two male types. However, reared females coupled with larval and pupal characters show this genus to belong to the family Odontoceridae of the leptocerid line. The larvae have several characters that are somewhat aberrant from known Odontoceridae and they will not key to any particular family in existing keys and diagnoses. Therefore, a new subfamily was erected for this genus.

Another manuscript on the immature stages of the larvae of the North American genera of Sericostomatidae (Trichoptera) is almost ready for submission. Although several European genera have been described there is not one description of the larvae of North American sericostomatids. Currently, all the North American species of Sericostomatidae are placed in one genus. However, discovery of the larval stages indicate that there are three genera in North America. Undoubtedly, one reason North American sericostomatids have remained so elusive is the rather unusual habitats occupied by the larvae. To date all the larvae have been found burrowing 0.5 to 2 cm below the stream bed in sand and fine gravel substrate. The larvae feed on fine detritus particles that are captured in the sand. In some areas as many as 23 larvae per sq. ft. have been found.

Another paper is also in progress on the larvae of the southeastern species of the genus *Brachycentrus* (Trichoptera: Brachycentridae). To date 5 species have been associated in the southeast.

Three species of the odontocerid genus *Psilotreata* have also been reared and a short manuscript is in progress on this genus.

A number of species of the Hydropsychidae genera *Cheumatopsyche* and *Hydropsyche* have been associated. However, these two genera are proving to be very difficult from several standpoints: (1) the larval stages are difficult to rear or get positive associations, particularly the less common species, (2) several species of larvae have few distinguishing characters, and (3) there are many more species present in the southeast than originally realized. We have 29 species in the above two genera from the Savannah River Basin alone.

These two genera are probably among the two most important genera of stream insects. Yet, they may well be among the last Trichoptera genera to have adequate keys to species.

An estimated 250,000+ specimens of adult Trichoptera were collected utilizing light traps throughout the southeast during the course of this study. About 1/3 of these have been identified to date. Undoubtedly, additional new material will turn up as these collections are sorted and identified.

SECTION V

DISTRIBUTION OF THE HYDROPSYCHIDAE IN THE SAVANNAH RIVER BASIN

The order Trichoptera, or caddisflies, constitutes 8 to 13% of all river fauna and the family Hydropsychidae represents approximately 80% (by number) of all stream Trichoptera larvae (Roback, 1962).

Previous workers have indicated that many factors were involved in the distribution of stream-dwelling caddisflies.

Ross (1963) reported that certain genera and species of Trichoptera were correlated with certain terrestrial biomes. The species associated with the temperature deciduous forest may be confined there by factors of shade, heavy autumnal fall of leaves, lower soil erosion load and lower streambank temperatures.

The species of the temperature deciduous forest were further restricted by stream size preference (Ross, 1963). A similar preference for a particular stream size was exhibited by the species studied by Ulfstrand (1968) in Lapland, Edington (1968) in England and Decamps (1968) in the Pyrenees.

Current was found to affect invertebrate populations directly through washouts (Minckley, 1963) and stability of water levels (Nelson and Scott, 1962). It was found to influence Trichopteran distributions directly and indirectly. Directly, current affected the distribution of the net-spinning Trichoptera through its influence on net building (Philipson, 1955; Scott, 1958) and efficient food gathering (Edington, 1968). Indirectly, it influenced trichopteran distribution through its effects on food distribution and size of substrate particles (Scott, 1958).

Ulfstrand (1967) found the microdistribution of benthic species to be most closely related to food preference. Macan (1962), Chutter (1963) and Ulfstrand (1968) attributed the increase in Trichoptera at lake outlets to increased planktonic content.

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According to Dodds and Hisaw (1925), Minshall (1968), and Armitage (1961), temperature was the major factor in faunal distributions. Decamps (1967) attributed the spatial distribution of the Trichoptera of the Pyrenees to the combined influence of altitude and temperature range.

Armitage (1958) also found a positive correlation between the relative density of Trichoptera and average alkalinity. Egglishaw and Morgan (1965) found the bottom fauna increased in number and weight in water with a total cationic content over 400 microequivalents/liter. Roback (1962) presented data showing that the two largest and most widely distributed genera of Hydropyschidae, *Hydropsyche* and *Cheumatopsyche*, were able to tolerate a wide range of ecological conditions. However, Roback's (1962) work was concerned only with the generic level, and the wide range of conditions tolerated by the above two genera may be partitioned by the individual hydropsychid species. The purpose of this study was to determine the habitat and range of individual species of the family Hydropsychidae in the Savannah River Basin in North Carolina, South Carolina and Georgia. The main factors evaluated were altitude, stream size and various water quality parameters. This study was also intended as an aide in locating various species in the southeast for rearing purposes.

Methods

A total of 57 stations was established along the length of the Savannah River and its headwaters and tributaries. Stations were selected to obtain a representation of both the main regions of the river's terrain and stream size. Thirty-one stations were established in the headwaters, fourteen in the Piedmont and twelve in the Coastal Plain. Figure 1 is a graph of station locations on the bases of stream size and altitude.

Both larval and adult collections were made. Larvae were collected by handpicking and dip-netting and most of them preserved in the field. Larvae of *Hydropsyche* and *Cheumatopsyche* were identified only to genus while larvae of the other genera were identified to species. Some mature larvae and pupae were maintained in ice chests and returned to the lab for rearing purposes. Little success was found in rearing larvae of Hydropsychidae; only pupal rearing was successful. Each specimen obtained was identified to species as a reared adult or as a pupa using the metamorphotype method. Imaginal collections were made with portable black light traps of the various stations from spring through early autumn. Most stations had at least 3 (some 4 or 5) light trap collections made in the spring, summer and early autumn in order to collect adults that possibly emerge at different times during this period. Traps were set up at dusk and run a minimum of 45 minutes most ran from 2 1/2 to 3 hours. Collections consisting of a quart or more of adults (several thousand individuals) were subsampled. For each of these large collections, a fifth of the sample was removed and identified. All adults were identified to species. For identification purposes, male and female genitalia were mascerated in KOH as outlined by Ross (1944). Approximately 100,000 adult Hydropsychidae were collected and examined during the study.

Water samples were taken in the field when either larval or adult collections were made. An attempt was made to obtain data on seasonal trends in water chemistry. However, due to the large number of stations, some stations have analyses for only three yearly values. For those stations having only three yearly values efforts were made to take at least one sample during mid-winter and mid-summer respectively. At one station the Environmental Protection Agency (EPA) operated a constant monitoring device.

Oxygen, temperature and chemical data utilized by our "grab" technique (of four yearly samples) compared closely with data from the EPA station.

General Survey of the River

The Savannah River is formed by the confluence of several headwater rivers in the southern Appalachian Mountains. The most important are the Tallulah and Tugaloo in Georgia, the Chauga, Keowee and Seneca in South Carolina and the Chattooga which courses through North Carolina, South Carolina and Georgia. The Tallulah and Chattooga merge and form the Tugaloo. The Chauga flows into the Tugaloo. The Keowee, rising as the Whitewater River in North Carolina, becomes the Seneca. The confluence of the Seneca and the Tugaloo forms the Savannah River. The Savannah River then courses between Georgia and South Carolina, flowing into the Atlantic at Savannah, Georgia. From the confluence of the Seneca and the Tugaloo, the length of the course is 502 kilometers. The total drainage basin area is 27,505 square kilometers (Patrick et al., 1967).

The headwater region has a steep gradient of 7.6 meters/kilometer, drainage basin area of 5,257 square kilometers and an altitudinal range from 1,067 to 201 meters (Patrick et al., 1967). The streams of this region are shallow and clear. They generally have a bed of rocks with some pool areas and their banks are heavily covered with vegetation.

The Piedmont region has an intermediate gradient of 1.0 meter/kilometer, a drainage basin area of 13,580 square kilometers and an altitudinal range from 201 to 36 meters. The Savannah River picks up most of its silt load in this area with the major contributor being the Broad River (Patrick et al., 1967). A major hydropsychid habitat in the Piedmont is the granite outcrop which is generally open to the sun and has thick Podostemum mats in areas of rapid current. Gradients of these granite outcrops varies from 10.6 meters/kilometer to 1.6 meters/kilometer (Hall, 1896).

The Coastal Plains region has an intermediate gradient in the upper region, a negligible gradient of 0.06 meter/kilometer in the lower region, a drainage basin area of 8,668 square kilometers and an altitudinal range from 37 meters to sea level (Patrick et al., 1967). The drainage basin's shape in the Coastal Plain is long and narrow with few major streams entering the Savannah River in this area. Tidal effects are noticeable inland as far as S58, the Savannah River at the end of route 275, Effingham Co., Georgia. However, these tidal effects do not reduce the current's velocity significantly beyond S59, the last station. Below the city of Augusta (located on the fall line between the Piedmont and Coastal Plain Regions), the substrate consists of sand and silt. Consequently, the limbs and logs that have fallen into the river have become the major habitats for larval hydropsychids. The small streams of the Coastal Plain are swampy, meandering and heavily wooded.

The impoundments are an important aspect of the Savannah River. They are located as follows: the confluence of the Tallulah River and the Chattooga River; Lake Rabun on Tallulah River; Yonah Dam on the Tugaloo River; Hartwell Dam on the Savannah River at U.S. Rt. 29; Clark Hill Dam at U.S. Rt. 221; Savannah River at Ga. Rt. 72; and the Savannah Bluff Lock and Dam below Augusta, Georgia.

Discussion

Definitions and Criteria

Since adult insects had to be used for specific determinations in the genera Hydropsyche and Cheumatopsyche, the stations of greatest abundance of a particular species outlined in Figs. 3-8 represent locations where a species usually composed 18% or more of the light trap catch at a particular station. Thus, one could be reasonably sure that larvae of these species occurred in the adjacent stream. A number of authors (e.g. Müller, 1966; Roos, 1957) have reported upstream migration of adult stream dwelling insects. One of us (Wallace, 1971) has also observed the same phenomenon in a species of Brachycentrus (Trichoptera: Brachycentridae). However, at several of our stations we ran light traps less than 3/4 kilometer upstream on a large tributary of a river and found few or no adults of species largely restricted to larger rivers in our traps (Table 3) nor were larvae of these species found in the adjacent stream. Conversely, both adults and larvae of these river species were abundant at the larger river station. It is interesting that the upstream adult flight and downstream drift of immatures or Müller's (1966) concept of the "colonization cycle" was questioned in regard to several European Hydropsyche spp. (Schuhmacher, 1970).

Stream sizes on the basis of drainage basin area were: springs, 0.1-0.9 km^2; brooks, 1.0-9.9 km^2; streams 10.0-99.9 km^2 and rivers, 100 km^2 and above. Figure 1 is a graph of the station locations on the bases of stream size and altitude.

Genera and their distribution

Seven of the eight eastern North America genera of Hydropsychidae were found in the Savannah River and its tributaries. They were Parapsyche, Arctopsyche, Hydropsyche, Cheumatopsyche, Diplectrona, Macronemum, and Potamyia. Parapsyche and Arctopsyche were found only in the streams and small rivers high in the headwater region. The genus Diplectrona extended from the highest altitude to the upper

Coastal Plain. It occurred in springs to the small rivers. *Hydropsyche* and *Cheumatopsyche* were the dominant genera of the river basin both in number of individuals and number of species. They extended from the lower headwater areas to the mouth of the river and occurred in all the stream sizes studied. *Macronemum* and *Potamyia* were found only in the Piedmont and Coastal Plain. They occupied primarily the largest rivers or largest drainage basin area.

Dominant species and their distribution

The species representing the genera that were monospecific for the study area were *Parapsyche cardis* Ross, *Arctopsyche irrorata* Banks, *Diplectrona modesta* Banks and *Potamyia flava* (Hagen). The last species will be considered with the subdominant species. *P. cardis* and *A. irrorata* were restricted to small springs and streams high in the headwater region. *P. cardis* (1067-244 meters; 0.4 to 20 km^2) (fig. 2) was found in greatest abundance at the smallest spring studied, S1 (1,067 meters; 0.4 km^2). Larvae of *P. cardis* were also found in the larger, turbulent Whitewater River (S7: 823 meters; 123 km^2). At this high an altitude, the temperature and oxygen regimes of this large river approached those of adjacent small streams. This species constructed nets combined with vegetable matter and was most often found on top of rocks in the full strength of the current. The area of greatest abundance for *A. irrorata* (fig. 2) was from 847 to 610 meters in altitude and from 4 to 74 km^2 in drainage basin area. In the headwater region common to both species, *A. irrorata* preferred larger streams than *P. cardis*. *A. irrorata* also constructed its net on top of rocks in the full force of the current.

D. modesta (fig. 2) ranged from the highest altitude to the upper Coastal Plain (1,067-46 meters) and occurred in the smallest streams to the smaller rivers (0.4-1,373 km^2). However, its limits of greatest abundance were 1,067-110 meters and 0.4-74 km^2. At lower altitudes *D. modesta* was found only in smaller streams and brooks where stream size did not exceed 40 km^2, i.e. S40, d.b.a. 13 km^2; S34, d.b.a. 36 km^2.

Macronemum carolina (fig. 2) was found in a few streams in the Piedmont, but was most prevalent in large rivers on the Coastal Plain. In this latter area, it was one of the more numerous species, i.e. 701 individuals at S54 on June 19, 1969. This species' abundance in the Coastal Plain was in contrast to that of its sister species *M. zebratum* (fig. 2) which was found only in small rivers of the lower region. The major habitat for the larvae of *M. carolina* was the fallen branches and tree limbs in the river. However, the larvae of *M. zebratum* constructed their nets along the lower sides of large rocks.

Within the genus *Hydropsyche*, *Hydropsyche sparna* Ross (fig. 3) and *Hydropsyche betteni* Ross (fig. 4) had a primarily mountainous distribution with a few extensions into the Piedmont. Both species inhabited all stream categories studied, but they were infrequent in the largest rivers. Preferred stream sizes were 0.4-843 km^2 for *H. sparna* and 0.3-414 km^2 for *H. betteni*. *H. betteni* was most abundant at stations with very solid substrates, i.e. 412 individuals from two collections at S33 which had an extensive granite outcrop and 1,777 individuals from three collections at S8 which had several large granite boulders on solid granite bottom. Larvae constructed nets in the thick *Podostemum* and moss growing in the swift current on these outcrops.

Both *Cheumatopsyche minuscula* (Banks and *Cheumatopsyche etrona* Ross (cf. figs. 6 and 7) inhabited the lower portions of the headwater region and the two species overlapped extensively in stream size and altitude preference. Although both species preferred streams and small rivers, *C. minuscula* was more abundant at lower elevations (251-229 meters) than *C. etrona* (488-229 meters).

The species *Hydropsyche venularis* Banks and *Cheumatopsyche analis* (Banks) ranged from lower headwaters to the mid- to lower Piedmont. The greatest numbers of *H. venularis* occurred in the rivers of lower headwaters and the upper Piedmont (253-159 meters; 187-1,373 km^2) (fig. 3). *C. analis* (fig. 6) was primarily a Piedmont species (244-37 meters) and its habitat ranged from the smaller streams (13 km^2) to the large sized rivers (19,446 km^2).

Cheumatopsyche pinaca Ross and *Cheumatopsyche pasella* Ross (figs. 6 and 7) were found from the lower headwater regions to the Coastal Plain. However, the above two species were ecologically separated to some extent by stream size preference. *C. pinaca* (fig. 7) preferred brooks to medium-sized rivers (0.4-1,036 km^2) and *C. pasella* (fig. 6) preferred small to large rivers, (1,373-22,404 km^2).

Hydropsyche incommoda Hagen and *Hydropsyche orris* Ross occurred in the lower elevations of the study area. *H. incommoda* (fig. 3) was a lower Piedmont-Coastal Plain species that inhabited large rivers. *H. orris* (fig. 4) was exclusively a large river and low altitude species.

As with M. carolina larvae, the major habitat for C. pasella, H. incommoda and H. orris larvae was the fallen branches and tree-limbs in the streams. Hydropsyche orris had the highest per cent composition in the area, i.e., 71% at S46, 42% at S47 and 38% at S50. At these three stations, H. incommoda did not exceed 20 per cent and C. pasella did not exceed 31%.

These dominant species fell into three main groups based on the lowest altitude tolerated by a species. These groups could then be subdivided on the basis of stream size preference or, again, on the basis of altitude (fig. 9).

A. Species that did not extend into the Piedmont or below 200 meters.

  A1. Species which inhabited springs and large streams primarily in the upper region of the headwaters.

    a) P. cardis (springs to large streams)
    b) A. irrorata (brook to large streams)

  A2. Species which inhabited large streams and small rivers primarily in the lower region of the headwaters.

    a) C. etrona
    b) C. minuscula

B. Species that did not extend into the Coastal Plains or below 37 meters.

  B1. Species which inhabited large streams and small rivers that arose in the upper headwaters (800-600 meters).

    a) H. sparna
    b) H. betteni

  B2. Species that inhabited brooks, large streams and small rivers in the upper portion of its range but restricted itself to the smaller streams in the lower portion.

    a) D. modesta

  B3. Species which inhabited large streams and small rivers that arose in the lower headwater (400-200 meters).

    a) H. venularis

C. Species that extended into the Coastal Plains region or below 37 meters.

C1. Species which inhabited streams to large rivers that began in the lower headwaters (primarily 600-200 meters).

a) *C. pasella*
b) *C. analis*
c) *C. pinaca*

C2. Species which inhabited large rivers at low elevations.

a) *H. incommoda*
b) *H. carolina*
c) *H. orris*

Subdominant species and their distributions

Several of the subdominant species were confined to the headwater region. *Hydropsyche morosa* Hagen, *Hydropsyche solossonae* Ross and *Cheumatopsyche gyra* Ross were found in brooks and small rivers. *H. solossonae* (960-823 meters) (fig. 3) was restricted to the upper portion while *C. gyra* (960-251 meters) (fig. 7) and *H. morosa* (896-213 meters) (fig. 5) extended into the lower reaches of the headwaters. The middle portion of the headwaters was occupied by *Hydropsyche carolina* Banks (832-488 meters) (fig. 3), *Hydropsyche scalaris* Hagen (736-46 meters) (fig. 3) and *Hydropsyche macleodi* Flint (732-518 meters) (fig. 3). *H. carolina* (37-228 km^2) and *H. scalaris* (37-526 km^2) inhabited streams and small rivers whereas *H. macleodi* was confined to brooks (4-9 km^2) (fig. 3). *Hydropsyche fattigi* Ross, *Hydropsyche demora* Ross (fig. 4), *Hydropsyche alvata* Denning (fig. 5), *Cheumatopsyche sordida* (Hagen) (fig. 8) and *Macronemum zebratum* (Hagen) (fig. 2) occupied the large streams and small rivers of the lower headwaters.

Cheumatopsyche enigma Ross, Morse and Gordon (fig. 7), *Cheumatopsyche geora* Denning, *Cheumatopsyche campyla* Ross and *Cheumatopsyche ela* Denning (fig. 8) extended from the headwaters to the middle of the Piedmont. Both *C. ela* and *C. campyla* inhabited large streams and medium-sized rivers whereas *C. enigma* and *C. geora* inhabited brooks and small rivers. *Hydropsyche bidens* Ross (fig. 5) inhabited the area from the headwaters to the lower Piedmont and occurred in both the smallest spring (0.3 km^2) and the larger rivers (19,446 km^2).

The only strictly Piedmont species were *Hydropsyche nr. scalaris* (fig. 3) and *Hydropsyche catawba* Ross (fig. 5). *H. catawba* ranged from 152 to 110 meters in altitude and 174 to 7,449 km^2 in stream size. *H. nr. scalaris* was found at a large stream low in the Piedmont near the fall line (S41: 38 meters; 73 km^2).

The subdominant species found primarily in the Coastal Plains were *Cheumatopsyche burksi* Ross (fig. 7), *Potamyia flava* (Hagen) (fig. 2) and *Cheumatopsyche virginica* Denning (fig. 8). The former two species primarily occupied large rivers; the latter species occupied large streams and large rivers.

Water quality

Table 1 lists the maximum and minimum values of water factors tolerated by some of the species. *P. cardis*, *A. irrorata*, *M. zebratum*, *M. carolina*, *D. modesta* and *P. flava* were included for their larvae could be identified to species. In the genera *Hydropsyche* and *Cheumatopsyche*, only those species with adults occurring at several stations in large numbers were used since they probably have their larvae occurring at or near the stations concerned.

The water characteristics analyzed could be divided into two groups: those without any trends and those that increased or decreased in value from the headwaters to the mouth of the river. The water parameters that had no particular geographical trends were ammonia, orthophosphate, total phosphate, sulfate, and pH. The minimum and maximum values for these were: ammonia, 0-2.26 ppm; orthophosphate, 0.06-2.45; total phosphate, 0.12-3.02 ppm; sulfate, 0-21.5 ppm; pH 5.57-8.85; velocity, 0-244 cmps (centimeters/sec). It should be emphasized that the velocity measurements were made in the main stream channels and are not necessarily reflective of the current speed passing over individual microhabitats occupied by hydropsychid larvae.

Generally the maximum velocity decreased along the course of the river, i.e. 244 cmps at S10 to 31 cmps at S57. This decrease in velocity may broadly influence the distribution of the hydropsychid larvae by its direct effect on net building and its indirect effect on the oxygen supply of the larvae. A decreased velocity engenders a low turnover rate in the water surrounding the larvae which results in a lower available oxygen supply. Hynes (1970) has reviewed much of the literature about increased current speed resulting in increased oxygen consumption by aquatic insects.

In all stream sizes studied, turbidity and conductivity increased from the headwaters toward the mouth of the river, i.e. S6 (847 meters; 10 km^2) with turbidities of 0-10 J.T.U. (Jackson Turbidity Units) and conductivities of 9.2-13.5 uohms; S40 (46 meters; 13 km^2) with turbidities of 8-31 J.T.U. and conductivities of 29-36 uohms. However, because the range of values tolerated by most species was wide, the main difference among species appeared to be the ability of species occurring at low altitudes to tolerate higher values constantly.

The remaining water parameters, water temperature, carbonate, nitrate and nitrite increased along the river course. The dissolved oxygen decreased. Superimposed on the main trend was a correlation between these water parameters and the types of species distributions (Table 2). Each distribution was correlated with a range of maximal values. Species of series A were found in streams with at low temperatures, a high minimal oxygen content and low values for nitrate, nitrite and carbonate. In the next two series, the species became more tolerant of high maximal temperatures, lower minimal dissolved oxygen content and increased nitrite, nitrate and carbonate content. This pattern of the water parameters reflecting the species preference in altitude and/or stream size was repeated within each series.

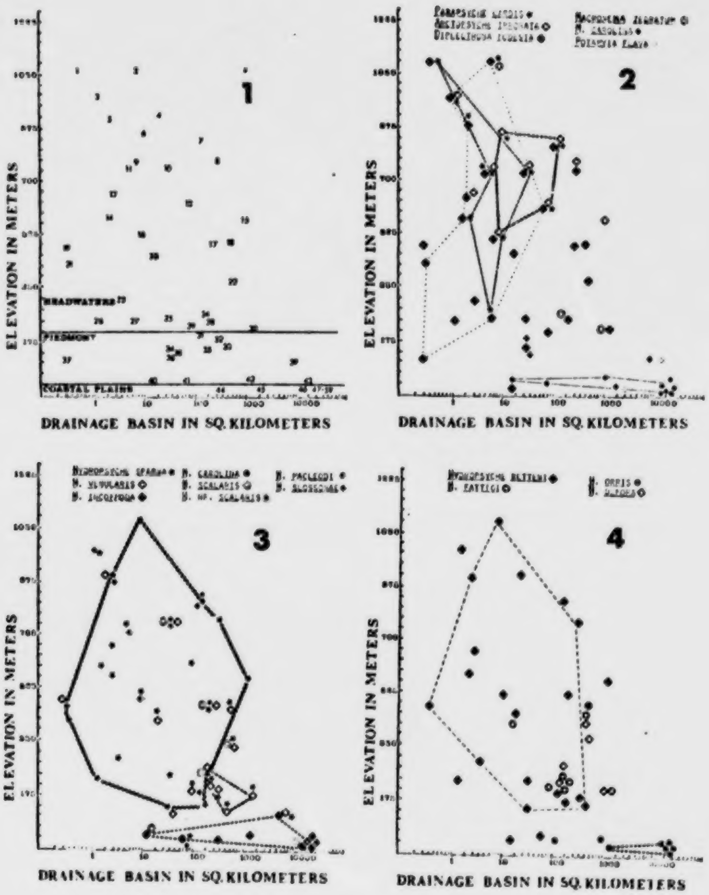
Annual maximum temperature and minimal oxygen concentrations which are linked to altitude and stream size seemed to be the most important of the water quality parameters affecting the distribution of the various species. The latter two items could be of considerable importance in regards to stressing the system by pollutants affecting the temperature and oxygen regimes. This may be especially important in the Piedmont and mountainous areas where many species were apparently restricted by maximum temperatures and minimal oxygen concentrations. Stressing these localities by a rise in temperature and/or a lowering of dissolved oxygen could possibly produce shifts in species towards those of the areas farther downstream. The effects of such a strain on the larger Coastal Plain streams cannot be surmised since these species were found at both the highest temperatures and lowest dissolved oxygen values throughout the study. Therefore, no apparent "limits" can be set for these species in regard to temperature and oxygen based on data in this study. However, stressing the larger streams of the Coastal Plain could possibly be even more catastrophic for the fauna since there are no "downstream" species to replace them.

The interaction of the species with all these chemical and physical factors, combined with current velocities, substrate and specific feeding habits, probably form an integrated web that influence the final distribution. A study of stations 30, 29 and 27 may indicate which factor or factors may have been more important in the distributions of some species. These three stations were within 1 kilometer of each other. Station 30 was located on the Tugaloo River 0.6 miles below Yonah Dam and S29 was located on Panther Creek 1 kilometer from Yonah Dam. S27 was a stream that fed into Panther Creek at S29. Table 3 lists the species found. The species distribution was not unusual. The river species occurred more frequently and more numerously at S30, i.e., *M. zebratum*, 1,764 specimens; *H. venularis*, 2,089 specimens; *C. analis*, 1,072 specimens. In S29, these river species either dropped out, i.e., *M. zebratum*, or they were greatly reduced in numbers, i.e., *H. venularis*, 101 specimens and *C. analis*, 23 specimens. Also, species which preferred streams appeared, i.e., *C. pinaca*, or increased in numbers, i.e., *C. minuscula* and *C. etrona*. Station 27 had a drastic reduction in the number of species. Here, the most abundant species were the ones preferring small streams, *D. modesta*, *P. cardis* and *C. minuscula*.

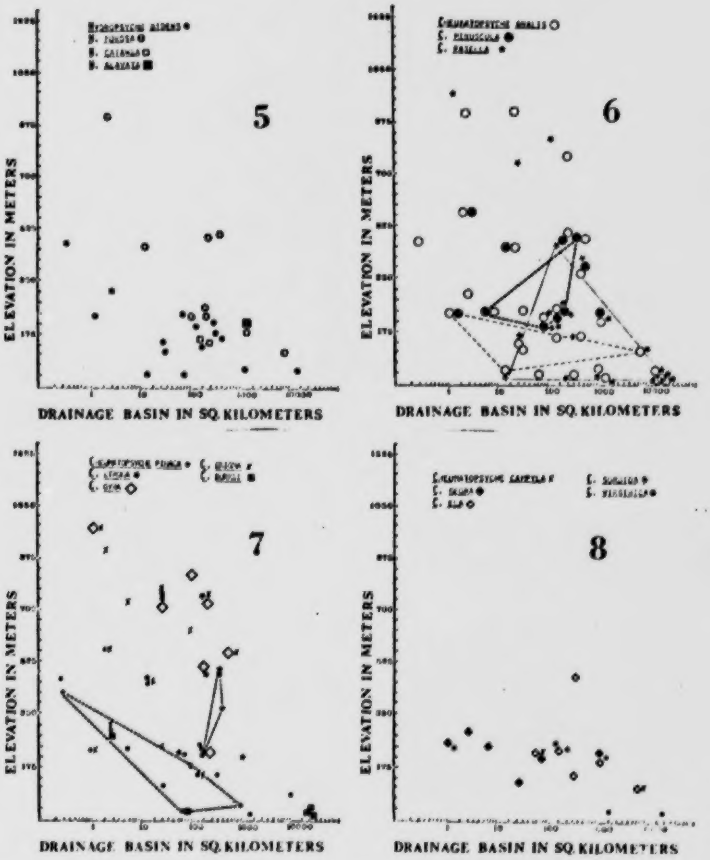
Table 4 lists the chemical and physical properties of these stations. The only factors that varied greatly were dissolved oxygen content and stream size. These stations were very similar in all other chemical and physical properties. Dissolved oxygen was the parameter varying most between Stations 30, 29 and 27. The Tugaloo River (S30) had a much lower minimum than either of the other two stations.

The other factor, stream size, varied greatly among these three stations. However, the importance of stream size was most strikingly demonstrated by a comparison of S29 and S27. Drainage basin area was the only factor that varied significantly between these two. Yet, the species composition varied the most between S29 and S27. Station 27 was dominated by *P. cardis* and *D. modesta*, species that preferred the smaller streams whereas S29 was dominated by *C. etrona* and *C. minuscula*, species that preferred larger streams and small rivers.

One important item that strict water quality parameters do not illustrate are the subtle differences in feeding habits of larvae. For example, Wallace and Sherberger (1973) recently found smaller particulate organic particle sizes in the Tugaloo River below the impoundment (S30) than in Panther Creek (S29). The Macronema zebratum larvae found only at S30 are microseston feeders and contain largely fine particulate organic matter, with some plankton and bacteria in their proventriculus which they filter from the water with extremely fine mesh nets with openings of about 5 X 40 u. These openings are much smaller than those found in the nets of other hydropsychid larvae at these stations. Such subtle differences in feeding habits of other species in this family are highly probable, especially in view of works by Sattler (1958, 1963), Kaiser (1965) and Schuhmacher (1970) on the nets and net making behavior of South American and European hydropsychids. Efforts are currently underway to investigate the roles of feeding and food availability on the distribution of several selected species in various genera in the Savannah River Basin. Distribution of various hydropsychid species may be influenced more by specific feeding habits and food availability than strict water quality parameters often utilized by aquatic biologists. This may be especially true in streams where environmental pollution is not a crucial factor.



Figs. 1-4. Fig. 1 - Distribution of the collecting stations (by station number) in the Savannah River Basin based on elevation and drainage basin size. Fig. 2-4 - Distribution patterns of various hydropsychid species in the Savannah River Basin. The outlined areas indicate areas of greatest abundance for a particular species, usually comprising 20% or more of the total Hydropsychidae collected.



Figs. 5-8. Distribution pattern of hydropsychid species in the Savannah River Basin. The outlined areas indicate areas of greatest abundance for a particular species, usually comprising 20% or more of the total Hydropsychidae collected.

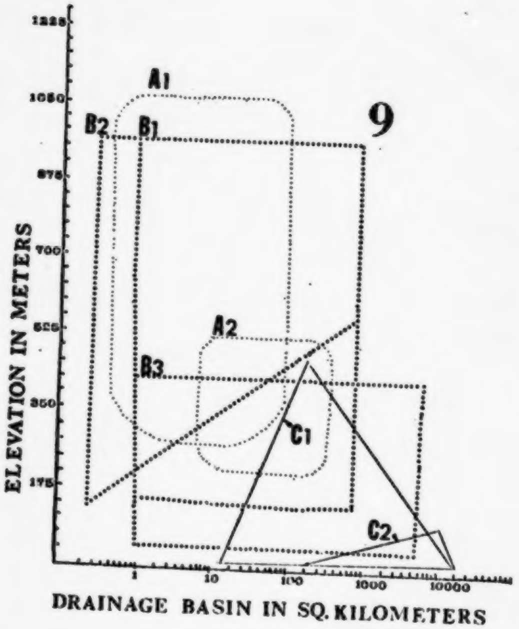


Fig. 9. Types of distributional patterns of the dominant species of Hydropsychidae in the Savannah River Basin. (See text, dominant species and their distribution).

Table 1. Range of Water Parameters Tolerated by the Dominant Species of Hydropsychidae in the Savannah River Basin for the Years 1968-69. The top figure represents minimum values; the bottom figure maximum. All items marked with asterisks are in parts/million.

	A. irrorata	*P. cardis*	*D. modesta*	*M. carolina*	*M. zebratum*
water temp. °C	1.7	1.7	1.7	7.0	3.6
	19.0	23.8	24.5	26.5	24.0
velocity cm/sec	23.5	34.4	22.9	33.5	41
	243.8	243.8	243.8	125.0	110
pH	6.0	6.0	5.8	6.0	6.4
	7.3	7.3	8.11	8.09	7.28
conductivity uohns at 25°C	8.9	8.9	8.9	16.5	11.5
	40.0	40.0	292.0	158.0	35.0
turbidity (Jackson units)	0	0	0	8	8
	42	59	180	101	30
*alkalinity (total)	5	5	5	10	10
	20	20	110	80	35
*NO_3	0.00	0.00	0.00	0.005	0.000
	0.526	0.635	2.127	2.791	0.396
*NO_2	0.000	0.000	0.000	0.00	0.000
	0.005	0.008	0.11	0.35	0.005
*NH_4^+	0.00	0.00	0.00	0.00	0.00
	0.914	1.17	1.75	2.26	0.40
*ortho-PO_4	0.00	0.00	0.00	0.00	--
	0.49	0.49	0.58	0.66	0.18
*total PO_4	0.20	0.20	0.16	0.20	0.02
	0.80	0.71	1.35	0.75	0.33
*SO_4	0	0	0	0	0
	9	6	9	11	3
*dissolved oxygen	8.0	7.7	4.4	4.8	5.5
	11.9	12.5	12.5	11.2	12.4

Table 1 (cont'd).

	P. flava	*H. sparna*	*H. venularis*	*H. incommoda*	*H. bettoni*
water temp.	6.6 26.5	1.7 26.5	2.5 26.5	6.6 26.5	2.8 25.5
velocity cm/sec	30.5 103.6	23.5 192.0	36.6 113.1	33.5 103.6	23.5 125.0
pH	6.60 7.55	5.57 7.55	6.35 8.04	5.88 7.71	5.88 8.09
conductivity uohms at 25^{o}C	31 108	8.9 92.0	10.8 158.0	23 132	8.9 158.0
turbidity (Jackson units)	12 88	0 180	4 180	8 101	4 157
*alkalinity (total)	10 70	5 35	5 80	10 70	5 80
*NO_3	0.005 2.791	0.038 1.914	0.038 1.843	0.005 2.791	0.000 1.914
*NO_2	0.00 0.35	0.008 0.100	0.000 0.008	0.00 0.35	0.00 0.11
*NH_4^+	0.30 1.89	0.00 1.58	0.00 1.28	0.30 2.23	0.00 1.58
*ortho-PO_4	0.00 0.61	0.00 0.58	0.00 0.50	0.00 2.45	0.00 0.58
*total PO_4	0.03 1.48	0.01 1.48	0.00 1.48	0.01 3.02	0.00 0.80
*SO_4	0 7	0.0 21.5	0.0 21.5	0.0 9.5	0.0 21.5
*dissolved oxygen	5.9 11.7	5.5 12.5	5.5 12.5	4.8 11.7	5.5 11.9

Table 1 (cont'd).

	H. *orris*	*C.* *pasella*	*C.* *analis*	*C.* *minuscula*	*C.* *pinaca*	*C.* *etrona*
water temp.	9.5 26.5	2.5 26.5	3.6 26.5	3.6 24.0	1.7 26.5	2.5 24.0
velocity fps	30.5 103.6	23.5 125.0	26.8 192.0	33.8 68.0	23.5 192.0	50.3 243.8
pH	5.88 7.50	5.57 8.09	5.88 8.09	6.35 7.49	5.57 8.09	6.35 7.28
conductivity uohm at 25°C	23 108	9.80 158.00	9.8 158	10.8 45.0	9.0 158	10.8 42
turbidity (Jackson units)	12 101	4 180	0 180	0 180	0 180	4 180
*alkalinity (total)	10 70	5 80	5 80	5 35	5 80	5 35
*NO_3	0.02 2.791	0.005 2.791	0.005 2.791	0.038 0.635	0.000 1.914	0.038 0.572
*NO_2	0.00 0.35	0.00 0.35	0.00 0.35	0.00 0.008	0.00 0.031	0.00 0.008
*NH_4^+	0.00 1.89	0.00 2.23	0.00 2.23	0.00 0.76	0.00 2.32	0.00 0.76
*ortho-PO_4	0.00 0.61	0.00 2.45	0.00 2.45	0.00 0.58	0.00 2.45	0.00 0.33
*total PO_4	0.01 0.75	0.01 3.02	0.01 3.02	0.01 0.64	0.00 3.02	0.02 0.80
*SO_4	0 8	0 21.5	0 21.5	0 4	0 21.5	0 9.0
*dissolved oxygen	4.8 11.1	4.8 12.5	4.8 12.5	5.5 12.5	5.2 12.5	5.5 12.5

Table 2. Range of water quality parameters associated with the type of distribution of the dominant species of Hydropsychidae in the Savannah River Basin.

Type of Distribution	Species	Water Temp. °C	Dissolved O_2 ppm	NO_2 ppm	NO_3 ppm	Total alkalinity ppm
A 1	*P. cardis*	1.7-23.8	7.7-12.5	0.000-0.008	0.00-0.635	5-20
	A. irrorata	1.7-19.0	8.0-11.9	0.000-0.005	0.00-0.526	5-20
A 2	*C. minuscula*	3.6-24.0	5.5-12.5	0.000-0.008	0.038-0.635	5-35
	C. etrona	2.5-24.0	5.5-12.5	0.000-0.008	0.038-0.572	5-35
	M. zebratum	3.6-24.0	5.5-12.4	0.000-0.005	0.000-0.396	10-35
B 1	*H. sparna*	1.7-26.5	5.5-12.5	0.008-0.10	0.038-1.914	5-35
	H. betteni	2.8-25.5	5.5-11.9	0.000-0.11	0.00-1.914	5-80
B 2	*D. modesta*	1.7-24.5	4.4-12.5	0.000-0.11	0.00-2.127	5-110
B 3	*H. venularis*	2.5-26.5	5.5-12.5	0.000-0.008	0.038-1.843	5-80
C 1	*C. pinaca*	1.7-26.5	5.2-12.5	0.000-0.031	0.00-1.914	5-80
	C. analis	3.6-26.5	4.8-12.5	0.000-0.35	0.005-2.791	5-80
	C. pasella	2.5-26.5	4.8-12.5	0.000-0.35	0.005-2.791	5-80
C 2	*H. incommoda*	6.6-26.5	4.8-11.7	0.000-0.35	0.005-2.791	10-70
	M. carolina	7.0-26.5	4.8-11.7	0.000-0.35	0.005-2.791	10-80
	H. orris	9.5-26.0	4.8-11.1	0.000-0.35	0.02-2.791	10-70
	P. flava	6.6-26.5	5.9-11.7	0.00-0.35	0.005-2.791	10-70

Table 3. Species Distribution and Total Number of Adult Specimens/Species at S30, S29 and S27.

Distribution type	S30	S29	S27
A 1	*P. cardis* (none)	*P. cardis* 3	*P. cardis* 18
A 2	*C. etrona* 5750	*C. etrona* 2964	None
	C. minuscula 395	*C. minuscula* 1386	*C. minuscula* 23
B 1	*H. sparna* 225	*H. sparna* 153	None
B 2	*D. modesta* 1	*D. modesta* 3	*D. modesta* 27
B 3	*H. venularis* 2089	*H. venularis* 101	None
C 1	*C. pinaca* (none)	*C. pinaca* 37	*C. pinaca* 3
	C. analis 1072	*C. analis* 23	*C. analis*
Head-water river species	*M. zebratum* 1764	None	None
	C. sordida 3	None	None
	H. fattigi 1846	*H. fattigi* 185	None
	H. alvata 16	None	None
	H. morosa 127	None	None
Piedmont river species	*C. ela* 348	*C. ela* 17	None
	H. bidens (none)	*H. bidens* 4	None
	C. campyla (none)	*C. campyla* 2	None
Piedmont stream species	*C. geora* (none)	*C. geora* 13	*C. geora* 1

Table 4. Chemical and Physical Properties of Stations 30, 29 and 27.

	S30	S29	S27
Water temp. °C	3.6-24.0	4.0-23.0	3.8-23.8
Velocity cm/sec	41-68	41	50
pH	6.4-6.9	6.8-7.0	6.8-7.1
Conductivity uohm @ 25 C	11.5-20.0	11.1-19.1	16.8-23.0
Turbidity (J.T.U.)	8-30	4-51	0-51
Alkalinity (total) ppm	10-20	10-20	10-20
NO_3 ppm	0.261-0.396	0.06-0.394	0.06-0.281
NO_2 ppm	0.000-0.003	0.000-0.006	0.000-0.005
NH_4^+	0.30-0.40	0.30-0.76	0.37-0.61
SO_4 ppm	absent	0-3	1-4
Dissolved O_2 ppm	5.5-10.4	8.3-12.5	8.1-12.0
Drainage Basin area km^2	1,373	84	7
Altitude, meters	213	229	244
Total PO_4 ppm	0.02-0.12	0.03-0.20	0.03-0.18

SECTION VI

DIELDRIN EFFECTS

A portion of the research time in this project was devoted to the analysis of residual levels of dieldrin and its effect on aquatic invertebrate populations in a tributary of the Savannah River in South Carolina.

A woolen mill that uses dieldrin as a moth proofing agent releases some of the pesticide (0.2 parts per million, ppm) in the plant's effluent, which in turn empties into a small Piedmont river in South Carolina. The number of species of aquatic invertebrates downstream in this river was greatly reduced and population complexes were altered. In all cases, dieldrin levels in internal extracts of specimens were higher downstream from the plant's effluent outfall than upstream. In some cases there was over a thousand fold increase in dieldrin residues in the downstream fauna compared to the upstream counterparts. Downstream the dieldrin residue, based on wet weights, was high as 24 ppm in *Simulium vittatum* Zett. larvae (Diptera: Simuliidae); 23 ppm in *Hydropsyche* sp. and 103 ppm in *Cheumatopsyche* sp. larvae (Trichoptera: Hydropsychidae); and 62 ppm in snails (*Physa* sp.). The following is an account of some of the completed work.

Contamination of many of our rivers and streams by pesticides is well documented. Lichtenberg et al. (1969) in a 5 year survey over the United States reported that the last 2 years of their survey reflected a decreasing trend in the use of persistent chlorinated hydrocarbon compounds. In their survey, dieldrin (1, 2, 3, 4, 10, 10-hexachloro-6,7-epoxy-1, 4, 4a, 5, 6, 7, 8, 8a-octahydro-1, 4-*endo*, *exo*-5, 8-dimethanonaphthalene) continued to dominate the pesticide occurrences in streams across the U. S., although its occurrence also had dropped in the last two years of their survey (1967-68).

Many "non-target" aquatic animals and even algae (Vance & Drummond 1969) are known to accumulate these pesticide residues in their tissues. Dieldrin and other chlorinated hydrocarbon insecticides are known to be readily absorbed into fatty tissues (Bridges et al. 1963). The amount of residue of any particular chlorinated hydrocarbon insecticide in animals varies greatly, depending upon the levels of exposure and the particular adaptations of the species. Ferguson (1969) has reviewed many of these adaptations.

There is a fair amount of information concerning chlorinated hydrocarbon residues in aquatic invertebrates, but there are little or no data concerning a specific location that has been subjected to a continued and prolonged exposure to a chlorinated hydrocarbon insecticide. In this work we compared dieldrin residues in several aquatic invertebrates collected upstream and downstream in the above situation.

All of the work in this study concerns the Rocky River in Abbeville Co., South Carolina. A woolen mill which has been in operation over 10 years near this river uses dieldrin as a moth proofing agent during the dyeing process which is conducted in large vats. The exhausted contents from these vats and rinse water from the yarn along with other process wastes is piped directly into a series of four oxidation lagoons. The effluent from these lagoons, about 1 million gallons per day, enters a small stream which in turn enters the Rocky River about 0.8 miles below the lagoons. The average discharge rate of the Rocky River is 307 cubic feet per second. The presence of dieldrin in the effluent from this mill has been documented by Dr. A. W. Garrison (personal communication) of the Environmental Protection Agency's Southeast Environmental Research Laboratory, Athens, Georgia. Garrison found the concentration of dieldrin in the effluent stream as it entered the Rocky River to be 0.2 parts per million (ppm); in the Rocky River just below its confluence with the outfall stream, 17 parts per billion (ppb); and in the Rocky River near its junction with the large Savannah River, about 5 miles below the plant outfall, 6 ppb. The above figures are based on averages obtained in water samples taken in March and October 1969. Lichtenberg et al. (1969) have reported concentrations of dieldrin in the Savannah River at North Augusta, South Carolina (some 50 miles downstream from this plant) averaging .085 ppb between the years 1964-68. This river was constantly in the top three most dieldrin-polluted rivers in the United States during the 5 year period in the above report.

The Invertebrate Fauna

In an effort to make some quantitative estimation of the invertebrate fauna of the polluted area, a series of Surber sq. ft. samples were taken on September 13, 1970. Station I (map) was a riffle area in Rocky River about 1/2 mile upstream from the junction with the small stream containing the dieldrin effluent. The bottom substrate at Station I was composed of large rocks on which a thick *Podostemum ceratophyllum* (Podostamaceae) mat was growing. Station II was on the "clean" side of the Rocky River opposite the small stream containing the dieldrin effluent. Station III was only 3.3 meters from Station II and just below the junction with the small effluent stream on the same side of the river as the effluent. Stations II and III were not true riffle areas but both stations had bottoms consisting of large rocks and a rather swift current (1.5 - 2.5 ft/sec). The rocks on the Station II side of the stream had a rather thick *Podostemum ceratophyllum* mat, those on Station III side had little or no *P. ceratophyllum* and a rather thick *Sphaerotilus* growth covered the rocks. Station IV was a riffle area (the first riffle area below the outfall) consisting of rocks and small stones. There was some *Sphaerotilus* and filamentous algae growing on the rocks at this location. The hellgrammite, *Corydalis cornuta* L. (Megaloptera: Corydalidae), *Hydropsyche* sp. (Trichoptera: Hydropsychidae), and *Simulium vittatum* Zett. (Diptera: Simuliidae) used for the April 18, 1970 downstream dieldrin analysis were removed from rocks in this riffle and from limbs and debris just upstream from this riffle. Station V was about 4 miles downstream from Station IV. The river was deeper and slower at this point. The steep banks were 10-20 feet high on either side of the river. The bottom was silty and there were no rocks. The nature of the bottom and the substrate to which the organisms were attached prohibited the use of the Surber sq. ft. sampler for quantitative sampling. The *Cheumatopsyche* sp. (Trichoptera: Hydropsychidae) and *S. vittatum* larvae obtained for dieldrin analysis on February 24, 1970, at this station were removed from treetops and debris that had fallen into the river. High water levels prevented aquiring enough *Cheumatopsyche* larave for dieldrin analysis on April 18, 1970 at this location.

The fauna list at the various stations in Table 5 is the result of 5 sq. ft. samples at Station I, 3 each at Stations II and III, and 5 at Station IV, taken on September 13, 1970. The invertebrates from all samples at each station were then converted to number per M^2.

Station I contained by far the greatest number of species. The Ephemeroptera, Plecoptera, Megaloptera, and Trichoptera fauna was severely reduced at the stations downstream from the textile plant outfall (Table 5). It should be emphasized that most of the Ephemeroptera that were found downstream were very small, perhaps indicating drift, such as that reported by Anderson (1967) and Elliott (1967) (6), cannot be eliminated.

Probably the most striking difference in the fauna occurred between Stations II and III. Though the stations were only 3.3M apart, the aquatic insect fauna at Station III was almost non-existent except for a few Chironomidae larvae. The only insects to show a downstream increase at Station IV were Chironomidae (Diptera) larvae and Empididae (Diptera) larvae. There were 8 Empididae larvae per M^2 found in the upstream (Station I) samples and 47 per M^2 were found in the downstream (Station IV) samples. The Chironomidae larvae went from 14 per M^2 upstream (Station I) to 4800 per M^2 downstream (Station IV), a 340 fold increase in the downstream (Station IV) fauna. The composition of the Chironomidae fauna changed between the various stations; at Station I it consisted of Calospectra sp., downstream at Station IV the fauna was composed largely of Polypedilum nr. scalaenum (Schrank). Among the non-insects, Oligochaeta increased downstream at Station IV (1600+ versus 22 per M^2 upstream at Station I).

Materials and Methods

Invertebrates used for dieldrin analysis were collected using standard aquatic dip nets. The specimens were placed in small plastic bags and frozen in dry ice in the field. The bags containing the specimens were transferred to a freezer after returning to the laboratory.

The number of individuals in each replicate for dieldrin analysis varied, depending upon the group involved. There were approximately 25-40 larvae of *Cheumatopsyche* sp. and *Hydropsyche* sp. in each replicate involving these two genera; 50-100 larvae of *Simulium*; 1 larva in each replicate of *Corydalis cornuta* L.; and 25-30 snails, *Physa* sp. in each of the downstream replications.

Extraction of Dieldrin in Samples -

Frozen samples were washed twice with 5 ml. portions of redistilled acetone for 30 seconds, air dried for several minutes, and then were weighed. A test was conducted and it was determined that no more weight loss occurred using acetone as a wash than using water. The analysis method is a modification of the procedures in the Pesticide Residue Analysis Manual (1969) of the Federal Water Pollution Control Administration. Samples were homogenized for 5 minutes in a Waring microblender containing 20 ml. of methanolethyl ether (1:1) and 1 gm. of anhydrous sodium sulfate. Each homogenate was taken to dryness with a rotary evaporator at 40°C and the residue was extracted 3 times with redistilled n-hexane. Dieldrin was partitioned into acetonitrile (analytical reagent) by extracting the hexane fraction 3 times with acetonitrile saturated with n-hexane. Acetonitrile was removed by rotary evaporation and the residue dissolved in petroleum ether (analytical reagent) and was cleaned up on a florisil column with 6% and 15% ethyl ether in petroleum ehter as the solvent system. In almost all cases dieldrin was in the 15% ethyl ether fraction. The column eluate was taken to near dryness, diluted initially to 5 ml with redistilled ethyl ether (these samples in petroleum ether interferred with GLC analysis), and stored at 7°C until analyzed by GLC.

GLC Analyses -

Analyses were conducted with a Varian Aerograph gas chromatograph (Model 2100) equipped with a ^{63}Ni electron capture detector. Five ul aliquots of all samples were injected in duplicate on each of two columns (glass, 6mm ID x 6 ft) packed with 5% OV-210 on 60/80 mesh chromosorb W (100 ml N_2/min; column temperature: 200°C) and with 1.5% OV-17 and 1.95% QF-1 on 100/120 mesh chromosorb W (120 ml N_2/min.; column temperature: 195°C). Dieldrin in appropriately diluted experimental samples was quantitated by comparing peak heights from linear standard curves obtained by injecting known quantities of analytically pure dieldrin intermittently with experimental samples.

Each of three groups of last-instar larvae of the Indian-meal moth, *Plodia interpunctella* (Hubner) (50 larvae/group), "spiked" with one ug of dieldrin was extracted and cleaned up as described above to obtain % recovery. Average recovery was 74%. Dieldrin was not detected in non-spiked *Plodia* samples.

Results and Discussion

Known dieldrin from two suppliers co-chromatographed with a compound in each of several selected experimental samples. The extremely large amount of compound in insects collected downstream and the smaller amount in insects upstream from the known source release of dieldrin supports the following conclusions that this compound is dieldrin. Also, Dr. A. W. Garrison (personal communication) has mass spectral evidence that dieldrin is present in the outfall stream.

In all cases dieldrin residue levels were higher in the downstream fauna than their upstream counterparts (Table 6). In *Simulium vittatum*, the average increase in the February collections was 1,178 fold downstream. In the April collections there was a 56 fold increase in the downstream *S. vittatum* compared to those upstream. The lower residues in the April collections of *Simulium* were probably due to their shorter period of exposure to dieldrin. The April *Simulium* larvae were small and represented a second generation that had been exposed only a few weeks, whereas the February larvae were the overwintering forms which had been exposed to dieldrin much longer. The highest residue levels in any of the animals occurred in the *Cheumatopsyche* downstream in Station V in the February collections. The dieldrin level in the two replications of *Cheumatopsyche* at this point ranged from 90 to 103 ppm (Table 6). Unfortunately no upstream *Cheumatopsyche* were analyzed, but in the closely related genus *Hydropsyche* the dieldrin residue level upstream was 0.171 - 0.685 ppm in the two replicates on the February date. On April 18, 1970, larvae of *Hydropsyche* were collected at Station IV and upstream at Station I. In two replicates there were 432 - 547 fold increases in dieldrin residues in the downstream *Hydropsyche* fauna compared to that upstream. The hellgrammite, *Corydalis cornuta* L., had the smallest amount of dieldrin of any organism tested downstream. The two downstream specimens of *C. cornuta* contained 1.213 and 0.920 ppm dieldrin, respectively. Despite this low level, the downstream specimens had a 60 fold increase over the upstream *C. cornuta*. In both upstream and downstream specimens, the larger two year old larvae had higher levels than the smaller one year larvae of *C. cornuta*. Downstream, *Physa* sp. snails had 33 to 62 ppm dieldrin. However, upstream there were few *Physa* snails but many *Goniobasis* sp. were present. The downstream fauna was composed almost solely of *Physa* sp.

These data indicate that there is a great deal of variation of dieldrin residue levels between various groups of organisms. Although the two genera of Trichoptera, *Hydropsyche* and *Cheumatopsyche*, are in the same family (Hydropsychidae) there was approximately a 4-5 times higher dieldrin content in the *Cheumatopsyche* downstream than in the *Hydropsyche* larvae. This may be due to any one or a combination of the following factors: 1-- Although both are reported to be omnivorous filter feeders there may be subtle differences between feeding habits in these two genera. 2-- There probably are physiological differences in regard to ability to cope with dieldrin or store the dieldrin in the body. The amount of dieldrin in the *Cheumatopsyche* larvae indicates that the *Cheumatopsyche* larvae are actually concentrating this insecticide in fat tissue at much higher levels than *Hydropsyche*. Perhaps this explains the absence of *Cheumatopsyche* larvae at Station IV. They possibly cannot cope with the higher dieldrin levels at this station as compared to Station V (levels based on water analyses, Garrison).
3-- There may be some differences attributable to the habitat. Many of the *Cheumatopsyche* larvae at Station V were recovered from limbs, etc., at the silty bottom of the river where there were possibly higher residues of dieldrin in the surrounding sediments. Holden (1965) reported that many chlorinated hydrocarbon insecticides such as dieldrin settle in such sediments. Holden also noted that levels of 0.5 ppm dieldrin in the mud may result in several fold increases of dieldrin in the invertebrate fauna living in such environments. 4-- Another possibility that should not be overlooked is the possible seasonal effect on residue levels. The downstream *Cheumatopsyche* were collected in February and the *Hydropsyche* in April. Kelso et al. (1970). found seasonal variations in DDT residues in fish, the lowest levels of DDT occurring in spring and summer.

One rather surprising result was the relatively low level of dieldrin found in the hellgrammite, *C. cornuta*. Gut analysis has revealed this animal to be a predator on other aquatic insects, including Trichoptera and Simuliidae larvae. With the reported increase in concentration of chlorinated hydrocarbons up the food chain, (Woodwell et al. 1967, Macek and Korn 1970), one would expect *C. cornuta* to have higher pesticide levels than its prey, yet it did not. Instead, the *Simulium* and hydropsychid larvae that represented probable prey had 12 to 70 times more dieldrin than the hellgrammite. This may be due to one of two things: either *Corydalis* does not store dieldrin or has some efficient mechanism for eliminating it. These data would support the findings of Keith (1966), Peterle (1966), and Chadwick and Brocksen (1969), that aquatic organisms may not necessarily show pesticide concentrations relative to their position in the food chain. Since Corydalis larvae were much less abundant downstream, they possibly represented recent migrants into the downstream area. However, the finding that both larvae analyzed downstream contained higher dieldrin residues than those upstream (Table 6) may discount this latter possibility.

One point that should be emphasized is that most of the animals with higher dieldrin concentrations discussed in this study are near the bottom of the food chain and are either detritus or omnivorous filter feeders. Judging from the relatively high concentrations of dieldrin in the Hydropsychidae and Simulium larvae and their exposure to their situation for several years, one may certainly surmise that they have developed some degree of resistance to this pesticide. Such resistant organisms that concentrate pesticides at these lower trophic levels could foreseeably represent real hazard to higher organisms that feed on them. This idea has been previously expressed by Naqvi and Ferguson (1968) and Ferguson (1967).

Since residues in the specimens examined in this study were several thousand times higher than residues found in the water, the possibility exists that such organisms as Hydropsychidae and Simuliidae larvae offer excellent possibilities as biological monitors for pesticides. For example, the Cheumatopsyche larvae at Station V had 103 ppm dieldrin compared to the water sample which had only 6 ppb. This represents a 17,000 fold concentration of dieldrin in Cheumatopsyche larvae compared to the water sample at Station V. The idea of using invertebrates as pesticide monitors was also expressed by Butler (1966) utilizing oysters and Bedford et al. (1968) using the freshwater mussel. This area should certainly be explored in greater detail.

Undoubtedly, much of the discrepancy between the amount of pesticide in the water and the organism is due to the low solubility of dieldrin and the fact that it settles to the substrate (Holden 1965) whereas most of the organisms discussed in this study are attached directly to or near the substrate or feeding on particulate organic matter and the chances are much greater that they will come into contact with higher concentrations of dieldrin than that normally present in the water. Nicholson (1967) has pointed out that monitoring to detect the presence of chlorinated hydrocarbon pesticides in water alone will not suffice due to the ability of pesticides to concentrate in such areas as sediments and aquatic organisms.

Figure 10. Diagrammatic map of Rocky River near Calhoun Falls, South Carolina.

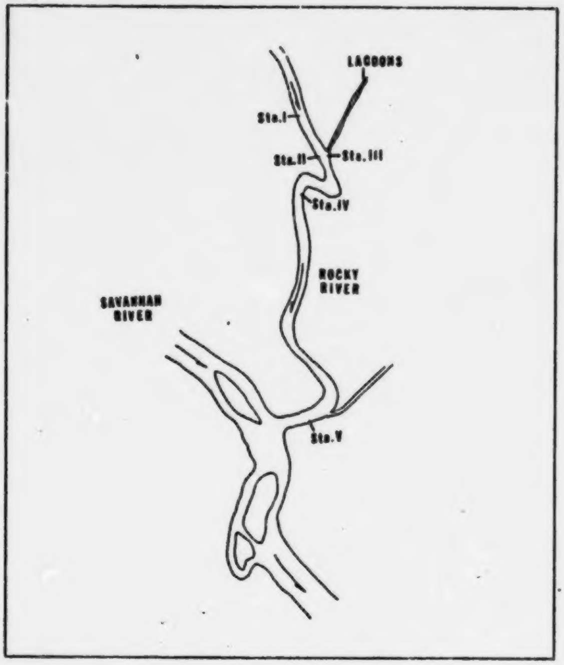


Table 5. Bottom fauna in numbers per M^2 in the Rocky River at Calhoun Falls, S. C. on September 13, 1970.

Organism		Sta. I	Sta. II	Sta. III	Sta. IV
Turbellaria		11	0	0	0
Oligochaeta		22	50	22	1600+
Insecta					
Ephemeroptera					
Ephemerellidae	*Tricorythodes* sp.	41	25	0	3
Baetidae	*Isonychia* sp.	92	0	0	1
	Pseudocloen sp.	32	40	0	0
	Undetermined	0	0	0	5
Heptageniidae	*Stenonema* sp.	5	7	0	1
Odonata					
Agrionidae	*Enallagma* sp.	3	0	0	0
Plecoptera					
Pteronarcidae	*Pteronarcys dorsata*	5	0	0	0
Megaloptera					
Corydalidae	*Corydalis cornuta*	27	0	0	1
Coleoptera					
Elmidae	*Macronychus* sp.	5	14	0	3
Trichoptera					
Psychomyiidae		3	0	0	0
Hydropsychidae	*Hydropsyche* sp.	527	65	0	12
	Cheumatopsyche sp.	57	40	0	0
Hydroptilidae		3	3	0	3
Leptoceridae	*Athripsodes* sp.	8	3	0	0
Diptera					
Chironomidae		14	47	15	4800+
Simuliidae	*Simulium vittatum*	84	58	5	19
Empididae	Nr. *Hemerodromia* sp.	8	0	0	47

Table 6. Dieldrin residues in certain aquatic invertebrates from the Rocky River, Abbeville Co., South Carolina.

				Dieldrin residue level (ppm wet wgt.)			
				Upstream[1]		Downstream[1]	
	Date	Stations	Replicates	OV-210*	OV17-QF1*	OV-210	OV17-QF1
Blackfly larvae							
Simulium vittatum	24-Feb.-70	I, V	2	.04	Trace**	19.44	23.03
				.19	.08	23.92	24.53
Simulium vittatum	18-Apr.-70	I, IV	1	0.26	.21	14.84	17.48
Caddisfly larvae							
Cheumatopsyche sp.	24-Feb.-70	V	2	no specimens- compare with *Hydropsyche* below		103.67	103.49
Hydropsyche sp.	24-Feb.-70	I	2	0.69	0.58	no specimens	
				0.17	.05		
Hydropsyche sp.	18-Apr.-70	I, IV	2	0.04	Trace	17.28	17.28
				0.03	Trace	18.01	23.22
Hellgrammite larvae							
Corydalis cornuta	18-Apr.-70	I, IV	2	0.02	Trace	1.21	1.48
				None	None	0.92	1.00
Snail							
Physa sp.	24-Feb.-70	V	2	no specimens		58.36	62.47
						33.24	37.41

[1] Upstream (Station I) downstream (Stations IV, V) - position from dieldrin source

* Gas chromatograph column (these figures were not corrected for percent recovery)

** Trace = less than 0.02 ppm

Current Status and Suggestions for Future Work Concerning Pesticide Studies

A large series of samples involving a variety of organisms were recently collected upstream and downstream in the Savannah River (as far as Savannah, Georgia). We are currently in the process of running residue analysis on these organisms to determine residual levels of dieldrin at various points upstream and downstream from this dieldrin source. However, a large scale in depth study is needed to relate dieldrin residues in the water, bottom substrate and debris and algae with the habitats and feeding habits of the various organisms.

It is rather appalling, especially with all the current concern over pesticide pollution, that few if any thorough studies exist, concerning pesticide movement in lotic waters, by a comprehensive study of pesticides in water, bottom substrate and debris, algae, aquatic invertebrates and higher organisms. The preceding data from the Rocky River in South Carolina indicates that certain snails (Physa sp.) and several aquatic insects are concentrating dieldrin up to 17,000 fold compared to water samples at the same location. Undoubtedly, much of the discrepancy between the amount of pesticide in the water and the various organisms is due to the low solubility of dieldrin and the fact that it settles to the substrate whereas many of the invertebrates in these streams are attached directly to or near the substrate feeding on particulate organic matter, greatly increasing the chances that the organism will come into contact with higher concentrations of dieldrin than normally present in the water.

Studies should be initiated to develop techniques that will allow specific invertebrates to be used as pesticide monitoring devices. If we have organisms that are concentrating pesticides several thousand fold above the concentration present in water, this will allow preliminary detection by relatively inexpensive gas chromatography equipment. The use of invertebrates also has several advantages over conventional techniques involving analysis of water samples alone. These are as follows: (1) The bottom substrate with attached organisms would probably not be as susceptible to the continual flushing action of the stream as water samples, particularly grab samples. (2) Due to the ability of certain aquatic invertebrates to concentrate pesticides several thousand fold over the concentration in the water, this would allow a pesticides detection whereas conventional water analysis may indicate only a trace or no detectable amount of the pesticide as being present at a particular time. (3) Since many invertebrates are relatively sessile, this would allow a technique that could help pinpoint a pesticide pollution source. Bottom organisms could possibly even aid in the detection of spots subjected to even periodic introduction of pesticides, whereas water samples alone, unless monitored constantly over a long period of time, might not detect such points of release.

It should be stressed that analysis of invertebrates will not replace conventional water analysis but will augment it. Higher concentrations of pesticides in animals at a specific location will serve as a tool in locating point sources of pesticide pollution. Conventional water analysis would have to be used to document if the area in question is currently active as a source of pesticide pollution.

SECTION VII

LEAF BREAKDOWN BY PELTOPERLA FEEDING

It has been realized for several years that many stream invertebrates rely on allochthonous organic matter as a food source. Nelson and Scott (1962) reported 66% of the energy of primary consumers on a Piedmont stream rock-outcrop was derived from allochthonous organic material consisting largely of autumn-shed leaves. They contributed this largely to bacteria, or the bacteria's conversion of leaf material to a metabolic product which could then be utilized by invertebrates. Minshall (1967) found allochthonous leaf material to be the most important food source of aquatic invertebrates in Morgan's Creek in Kentucky. Hynes (1963), Kaushik and Hynes (1968) suggested that much of the feeding of aquatic invertebrates on dead leaf material may be direct. Egglishaw (1964) has convincingly shown that the distribution of aquatic invertebrate bottom fauna is closely associated with plant detritus that accumulates in streams. Ross (1963) reported that Trichoptera distribution often parallels that of terrestrial biomes. Ross attributed much of this distribution pattern to the annual leaf fall which is utilized as a food source by many Trichoptera larvae.

The order Plecoptera is divided into 2 suborders, the Setipalpia and Filipalpia. In general, the naiads of the Setipalpia are regarded as being carnivorous and those of the Filipalpia are phytophagous (Brinck 1949). Brinck (1949) and Hynes (1941) were among the few workers to report on the actual feeding habits of filipalpian naids. Referring to Capnia spp. and Nemoura spp. in Sweden, Brinck makes the following statement: "Usually the nymphs are seen sitting quietly on the dead leaves which they skeletonize." Most of the other work on stonefly feeding habits is based on descriptive gut analysis. With the phytophagous species using this method, it is difficult to evaluate precise feeding habits.

The family Peltoperlidae of the Filipalpia has only one genus, Peltoperla, according to Ricker (1952). The genus is subdivided into several subgenera of which the subgenus, Peltoperla (P.) maria Needham and Smith, is extremely abundant in the southern Appalachian Mountains.

Peltoperla maria is probably the most abundant stonefly species in the southern Appalachians. Tebo and Hassler (1961) found *P. maria* the dominant stonefly species in Western North Carolina trout streams. Claasen (1931) made the following statement about *Peltoperla* spp. naiads: "The nymphs of this genus are herbivorous and are usually found in small fresh-water spring brooks where the current is quite slow and where dead leaves and debris accumulate. In such localities *Peltoperla* may usually be found in considerable numbers." We have found (unpublished results) that in such localities the numbers may exceed 50 per ft.^{2}, especially where there is a mixed deciduous forest cover surrounding the stream.

While collecting from the above types of habitats we noticed many of the leaves in the streams were skeletonized in areas where *Peltoperla* naiads were abundant. There appeared to be definite preferences for leaves of certain plant species. The purpose of this paper is to present some observations on the laboratory feeding habits of *P. maria*, including some of their preferences and amounts of material consumed.

Materials and Methods

Half to nearly full-grown naiads of P. maria were collected at the Coweeta Hydrological Laboratory, Macon Co., N. C., using dip nets. The naiads were maintained in the laboratory in 12" x 6" x 4" plastic trays with aerated H_2O and leaf material at 15°C until ready for use. Newly fallen leaves were collected from the Coweeta site, washed and preleached in a tank of aerated H_2O for 10 days. After 10 days the leaves were removed, dried in an oven at 100-101°C for 24 hours and then transferred to desiccators until a constant dry weight was reached. Leaves were stored in desiccators until ready for use. Each species of leaf was then weighed into individual portions consisting of about 500 mg each, using a Mettler H-16 balance. Five different species of leaves, each consisting of approximately 500 mg portions, were placed in plastic trays 12" x 6" x 4", supplied with 2 liters of stream water from the Coweeta site. The plastic containers were covered and a small hole was cut in each top to supply an airstone. Both containers with and without Peltoperla were aerated. Fourteen containers were utilized for each series of 5 leaf species used. Four of the containers had only leaves and water to obtain correction values for leaching; the remaining 10 containers had leaves, water, and 50 P. maria in each container. To insure good wetting, 24 hours prior to the addition of Peltoperla, leaves were placed in the control and feeding containers with 21 of H_2O. All experiments were conducted in the dark in BOD incubators at 15°C. The containers were carefully examined daily to insure that an adequate supply of each species of leaf was present and to remove any exuviae or dead Peltoperla. Mortality rates did not exceed 10% during the two week period. Any dead Peltoperla or exuviae were removed and dried and ashed in a muffle furnace to correct the final weights at the termination of the feeding experiment. After two weeks the Peltoperla and leaves were removed from the containers, dried in an oven at 99-100°C for 24 hours, and placed in desiccators with $CaSO_4$ until a constant dry wt. was reached. The weights were recorded and the Peltoperla were ashed in a muffle furnace at 550°C for an ash free dry weight. The water from each container was filtered using Whatman #5 paper to remove frass and adjusted with the original stream water to a volume of 2 1 to correct for slight evaporation losses. A tannin and lignin content of the water was analyzed using the tungstophosphoric and molybdophosphoric acid method (APHA 1965). Colorimetric analysis was conducted on a B & L

Spectronic 20. It should be emphasized that this test is not specific for tannin and lignin since other reducing materials present may give similar responses. Therefore, results are expressed as tannin acid-like substances.

The three groups, each consisting of 5 species of leaves, utilized in the study were as follows: group I, white oak *Quercus alba* L.; Sycamore, *Platanus occidentalis* L.; Alder, *Alnus serrulata* Willd.; Sweet gum, *Liquidamber styraciflua* L.; and dogwood, *Cornus florida* L.; group II, sourwood, *Oxydendrum aboreum* L.; American beech, *Fagus grandiflora* Ehrh.; tulip poplar, *Liriodendron tulipifera* L.; red maple, *Acer rubrum* L.; and *Rhodendron maximum* L.; group III, winged elm, *Ulmus alata* Michx.; hickory, *Carya ovata* K. Koch; Chestnut Oak, *Quercus prinus* L; blackgum, *Nyssa sylvatica* Marsh; white pine, *Pinus strobus* L.

Results

When placed in containers with the leaf material, Peltoperla naiads would congregate on the blades of certain leaves. Those leaves on which they congregated generally represented the leaves most preferred as food. The insects do not penetrate entirely through the leaf with one bite, but apparently rasp the plant tissue away gradually, avoiding the xylem and phloem. They fed on the cuticle, epidermis, and mesophyll of the leaves, leaving most of the vascular bundles or venation intact. This results in the characteristic skeletonized appearance of the leaf.

Of the leaves in group I (dogwood, sweetgum, alder, white oak, and sycamore) alder and dogwood were preferred by P. maria (Table 7). White oak was the least preferred in this group. The data was treated using the method of M rankings as reported by Norman and David (1969). It was found that alder was significantly high at the .01 level, dogwood at the .05 level, and white oak was significantly low at the .01 level (Table 8). Sweetgum and sycamore preferences were between these extremes. In 7 out of 10 containers alder was eaten at the highest rate, followed by dogwood in 2 and sweetgum in 1 of the remaining 3 containers. White oak was consumed at the lowest rate in 7 of 10 containers, followed by sycamore in 3 of the containers.

The leaves in group II consisted of sourwood, tulip poplar, American beech, red maple, and Rhododendron. Sourwood leaves were consumed at a rate significantly high at the .01 level, followed by tulip poplar, red maple, and American beech, while Rhododendron was significantly low at the .01 level. Sourwood was the preferred leaf in 8 out of 10 containers with American beech and red maple preferred in 1 container each. Rhododendron was consumed at the lowest level in 8 of 10 containers, followed by American beech in the other two containers.

Group III consisted of leaves of elm, chestnut oak, blackgum, hickory, and white pine needles. Of these, elm was the preferred food of P. maria. The consumption of elm was significantly high at the .01 level followed by blackgum and hickory. Chestnut oak and white pine were eaten at rates significantly low at the .05 and .01 levels, respectively. Elm was the preferred leaf in all 10 containers. The least preferred plants were white pine in 5 of 10 containers followed by chestnut oak in 4 and hickory in the remaining container.

Tannin and lignin-like compounds (expressed as tannic acid) analysis on filtered H_2O from the containers in groups II and III revealed a higher average tannic acid content in the water from containers where Peltoperla had been feeding than in the controls. The H_2O from feeding experiments in group II averaged 1.6 ppm tannic acid contents versus 1.35 ppm for the control containers at the end of the 2 week period. The water of group III feeding containers averaged 2.5 ppm versus 2.1 ppm tannic acid for the controls. The tannic acid content of the original stream water used in the experiments was 0.1 ppm. The data from group I was discarded since this H_2O sat in the lab for several weeks prior to analysis and several containers developed heavy growths of bacteria, whose effects on the readings were unknown.

Discussion

In the southern Appalachian Mountains and higher elevations of the Piedmont Plateau, P. maria naiads are much more abundant in the smaller streams that drain deciduous forests. Woodall (unpublished data) has found P. maria much more abundant in mixed hardwood forest watersheds than in adjacent pasture and white pine watersheds at the Coweeta Hydrological Laboratory, Macon Co., N. C. Undoubtedly, this is due partly to the availability of leaves as a food source. Knight and Gaufin (1966) studied the effects of altitude on stonefly distribution in the Rocky Mountains and found Setipalpia to be much more abundant at higher altitudes than Filipalpia. They concluded that part of this effect may be due to feeding habits. From our data one may certainly surmise that leaf litter accumulations in H_2O could affect distribution of many herbivorous species. In addition to our observations on Peltoperla, several other groups of aquatic insects such as naiads of several Stenonema spp. (Ephemeroptera: Heptageniidae) and several Tipula spp. larvae (Diptera: Tipulidae) have been observed feeding in a similar manner. This lends support to Ross' (1963) and Hynes' (1963) ideas that distribution of aquatic insects is often related to terrestrial biomes or forest cover types.

The possibility exists that at least a portion of the food of herbivorous insects such as Peltoperla may consist of bacteria or fungi growths which accumulate on the surface of the leaves after they fall into streams. However, a series of gram stains made on the gut contents of several P. maria nymphs yielded no evidence that there were enough bacteria present to contribute significantly as food for the insects. Hynes (1963) (1968) reported that although much of the feeding of aquatic invertebrates on leaf material may be direct, the possible importance of bacteria and fungi should not be overlooked. It is very interesting that Hynes (1963) found leaves of alder and elm to be very high in nitrogen content. In our study both of these species were consumed readily by Peltoperla. Satchell and Lowe (1967) reported alder and elm to be the preferred litter in selection tests with the earthworm Lumbricus terrestris. Hynes (1968) found that leaves of various plant species may behave differently in H_2O and he suggested that the temperature and type of microflora associated with various leaves may play an important role in the nutritional value of leaves. Detailed study of the microflora associated with the various leaves used in our study has not been done; certainly this should be an area for further investigation as well as the effect of "aging" leaves for various periods of time in H_2O.

Other areas that should be investigated further are the possibility that age of the naiads and different combinations of leaves may influence feeding habits. In our experiments we utilized naiads that were half- to full-grown. The possibility remains that feeding habits of earlier instar naiads may differ from the older naiads. However, we saw no evidence of different leaf preferences between half- and full-grown naiads in our study. The possible effects of different leaf combinations, i.e., those that were consumed at the highest or lowest rates across the three groups could prove very interesting.

The higher tannin and lignin content of the water with Peltoperla is probably due to increased leaching from the fecal pellets. The finely ground fecal pellets could probably be subject to more leaching than the intact leaves. When filtered, dried, fecal pellets were placed in beakers of H_2O, there was a noticeable increase in the tannin- and lignin-like compounds in this H_2O within a 24 hour period.

The finely ground leaf material in these fecal pellets may be carried downstream by water currents more readily than intact leaves which are often retained by obstructions or pool areas in streams. The fecal pellets may be available as food to downstream filter or detritus feeders, as well as bacteria and other microorganisms. Plans are underway to evaluate this possibility.

Although the exact role of the microflora is unknown, obviously the feeding of aquatic insects such as Peltoperla aids in alleviating part of the overall organic load placed on streams annually by autumn-shed leaf material. The leaching of Peltoperla feces would contribute to the dissolved organic content of stream water; simultaneously, the small fecal pellets could be readily carried downstream by the water currents. Either of these two or their combination could possibly influence downstream water quality, decreasing the organic load due to intact leaf material in headwater regions of streams. Though the contribution of individuals of P. maria may be slight, when one considers the large number of these and other insect species that may be feeding in a similar manner, the effect undoubtedly becomes significant.

Table 7. $\bar{X}$ gm of Leaf material eaten/gm dry wt. Peltoperla/2 week period[1]

Leaf	gm eaten[2]/gm *Peltoperla*[3]
alder	.5983
dogwood	.5175
sweetgum	.2475
sycamore	.1271
oak	.0996
Avg. Total - Group I	1.5900
sourwood	1.0454
tulip poplar	.3815
red maple	.2611
American beech	.1640
Rhododendron	.0297
Avg. Total - Group II	1.8818
elm	.6217
Blackgum	.2510
hickory	.1268
chestnut oak	.0654
white pine	.0425
Avg. Total - Group III	1.1074

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[1] each value represents an average of 10 treatments corrected for leaching

[2] dry wt.

[3] ash free dry wt.

Table 8. Ranking[1] of leaves according to consumption of *Peltoperla* maria naiads (gm dry wt leaf material eaten[2] gm dry wt insect).

Group I	Alder *Alnus serrulata*	Dogwood *Cornus florida*	Sweetgum *Liquidamber styraciflua*	Sycamore *Platanus occidentalis*	White oak *Quercus alba*
Ranking	45##	41#	29	20	15**
Group II	Sourwood *Oxydendrum aboreum*	Tulip poplar *Liriodendron tulipifera*	Red maple *Acer rubrum*	American beech *Fagus grandiflora*	Rhododendron *R. maximum*
Ranking	48##	38	28	24	12**
Group III	Elm *Ulmus alata*	Black gum *Nyssa sylvatica*	Hickory *Carya ovata*	Chestnut oak *Quercus prinus*	White pine *Pinus strobus*
Ranking	50##	39	28	18*	15**

[1] See Norman & David (1969) (max. ranking sum = 50; min. ranking sum = 10)

[2] Corrected for leaching

##Sig. high at .01
#Sig. high at .05
**Sig. low at .01
*Sig. low at .05

SECTION VIII

EFFECTS OF FOREST COVER ON INSECT DISTRIBUTION

In the introduction to the previous section it was evident that detritus, especially autumn shed leaf material, can be a very important source of energy to stream insects. In small headwater streams this probably represents, by far, the most important food source available to stream invertebrates. The purpose of the following study was to compare the effects of surrounding terrestrial forest cover types (Hardwood, Coppice Hardwood, White Pine and Old Field) on the benthic fauna of 4 small springbrook communities in the Southern Appalachian streams.

Study Area

The U.S. Forest Service established the Coweeta Hydrologic Laboratory in 1934. It is located in the Southern Appalachians in Western North Carolina.

Four watersheds were selected within an area of less than 1 sq. mile. They were named Old Field, Hardwood, White Pine, and Coppice. The first three faced northwest and drained into Ball Creek. The latter faced east and drained into Shope Fork.

In the Old Field watershed, stream bank vegetation growing up to 15 feet elevation above the flowing channel was removed by clearcutting (12% of the watershed area) in 1941. Regrowth was allowed until 1958 when the forest was clearcut and converted over a 3 year period to Kentucky 31 fescue. The conversion was accompanied by heavy application of lime and NPK and, in March 1965, the grass was refertilized with NPK. The grass cover was killed and maintained virtually free of vegetation, except for a narrow (3 m) band along the stream, in 1966 and 1967 by use of Atrazine and Paraquat. Since April of 1968, vegetation on the watershed has been allowed to revert naturally toward a hardwood forest.

The Hardwood watershed vegetation had not been disturbed since the laboratory was established. *Liriodendron tulipifer* L., *Quercus rubra* L., *Carya* spp., *Taxus canadensus* (L.) Carr. and *Rhododendron* spp. were predominant along the stream margins.

On the slopes *Quercus* spp., *Carya* spp., *Rhodendron* spp., *Kalmia latifolia* L., *Acer rubrum* L., *Myssa sylvatica* L., *Oxydendrum arboreum* (L.) DC. and *Cornus florida* L. were the most common plant species.

In 1942 all forest and shrub vegetation on the White Pine watershed was cut but not removed. From 1943 to 1955, a low herbaceous and shrub cover developed and was maintained by annual clearcuttings. In 1956 white pines (*Pinus strobus* L.) were planted. Despite attempts to control hardwood regrowth by cutting, a dense growth of *Liriodendron tulipifera* L., ferns, *Rubus occidentalis* L., and *Rhododendron* spp. developed along the stream.

During 1939 and 1940, all woody vegetation on the Coppice watershed was cut and left in place. A coppice forest was allowed to regrow, and a similar cut was made in 1962. The woody vegetation in this watershed included *Liriodendron tulipifera* L., *Quercus rubra* L., *Carya* spp., *Taxus canadensus* (L.) Carr., *Rhododendron* spp., *Kalmia latifolia* L., *Acer rubrum* L., *Nyssa sylvatica* L., *Oxydendrum arboreum* (L.) DC., and *Cornus florida* L.

The substrate in the four watersheds consisted of sand and flat granite rocks to 25 cm in diameter. The rocks in the Old Field stream were generally covered with more sand than those in the other watersheds. The Old Field stream flowed over a large granite outcrop in one area which was intermittently barren or covered with moss. There were many small barren outcrops in the Coppice stream. At the base of each waterfall formed by these outcrops was a pool with a sand bottom. Some of these waterfalls approached 2 m in height.

The streams were about 1/2 m wide in the sampling area but occasionally their width approach 2 m. Water depth ranged from less than 3 cm in areas where the stream bed was wide to about 15 cm in narrow areas.

Methods

The lower portion of each stream was divided longitudinally into four sections. Due to the irregular relief of the area, the stream beds were not measured precisely but were measured approximately by paces. Above approximately 400 paces sampling was impractical because the stream bed was narrow and filled with debris.

A stratified random sampling technique was used. Each month one number was selected from a table of random numbers and used as an index for sampling sites along the streams. For example, if 35 was the number chosen, then samples were collected at 35, 135, 235, and 335 paces from the weir site. The same set of numbers was used on each watershed. Sampling began at the weir and proceeded toward the source so that no substrate was disturbed before it was sampled. Thus one sample was collected from each 100-pace section of each stream monthly between 12 August 1968 and 18 July 1969. A surber sampler (Usinger, 1963) with a nylon mesh of 43 threds per inch was used for sampling. The sampler was placed in the deepest part of the stream at each location and the substrate within the sampler was disturbed by hand. Attached plants and animals were removed from large rocks with forceps and allowed to wash into the net. The sampler was removed from the stream when it appeared that all detritus and benthic organisms had been washed into the net. Samples were then transferred to a plastic bag, stored in crushed ice and returned to the lab where they were processed within 24 hr. Each sample was washed in a sieve of 10 meshes/cm and the retained portion was placed in a white enamel tray where the organisms and detritus were picked out by hand. Ash-free dry weights were obtained according to the method used by Nelson and Scott (1962).

Dissolved oxygen, pH, and temperature were measured in the four streams each month. The measurements were taken immediately above the weir ponds. Stream temperature and dissolved oxygen data were obtained with a YSI oxygen-temperature probe and pH was determined with a Hellige kit. Turbidity and alkalinity analyses were conducted using Hach reagents and a Bausch and Lomb "Spectronic 20" spectrophotometer. Conductivity was measured with a Hellige conductivity meter.

Results and Discussion

Dissolved Substances

Very small quantities of dissolved minerals were found in the water at Coweeta. Results are reported in Tables 9 and 10 Lowest values were recorded in the Hardwood stream and highest values were in the Old Field stream. The Old Field stream was most turbid and the Hardwood stream was least turbid. The low turbidity, conductivity and alkalinity values indicate the nature of the Coweeta streams. pH was generally constant reflecting the chemical stability of these streams.

Dissolved oxygen values increased in all the streams as solubility of the gas increased during the winter months. No consistent differences were noted among the streams. The lowest values were recorded in August and the highest values were recorded in December.

Temperatures

In every month except January, the Old Field stream was warmer than the others. This was attributed to two factors: the absence of shade and the time the readings were taken, which was about 2 P.M. Swift and Messer (1971) reported increases of up to 8 C where forest trees and understory vegetation were completely cut. Even in winter, the Hardwood stream was heavily shaded by dense Rhododendron growths and the Pine stream was heavily shaded throughout the year. These two streams consistently had the lowest temperatures. In all streams temperatures were highest in August and lowest in December. It should be emphasized that the temperatures in Table 1 are not means, but were recorded at the time of sample collection.

Detritus

The standing crop of detritus in Coweeta streams is summarized in Table 11. In the Old Field stream the source of detritus was primarily grasses and grass roots. Mosses were present on wet rock outcrops, but their biomass was significant only in warmer months when there was little detritus contributed by grasses. Sparse growths of Rhododendron spp., Rhubus occidentalis L. and other shrubs also contributed to detritus.

Detritus in the Hardwood stream consisted mainly of leaves from deciduous trees and Rhododendron. Rhododendron leaves comprised almost 1/2 of the detritus and chestnut oak accounted for a large portion of the remainder.

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In the Pine stream detritus was composed of both deciduous leaves and pine needles. Dead needles remained in the trees and contribute detritus to the stream all year. Some grasses, *Rhododendron*, and other littoral, woody growth also contributed to detritus.

The source of detritus in the Coppice stream was primarily deciduous leaves mixed with some *Rhododendron*. Sparse growths of grasses along the stream banks also contribute to detritus accumulation. In samples taken from granite outcrops, most of the vegetable material was moss and very few recognizable leaf fragments were present.

Bottom Fauna

Since it was difficult to qualify the sizes of these small streams and since the turnover time for all the organisms was not similar, a relative importance value (Ball, et al., 1969) rather than absolute number was used for comparisons. This value is the product of the per cent by weight and per cent by number for each group of insects. (Table 12)

Homogeneity of total numbers among watersheds was tested for each taxon using a Duncan multiple-range test. Non-insects were not included. The results (on the taxa for which the test was valid) are shown in Table 13. The monthly mean standing crops of numbers and biomass (ash free dry weights) for the 16 most important organisms, are presented in Table 14.

The importance values for each species were averaged for the four watersheds and the 16 most important organisms were included for discussion. Four "minor" organisms which exhibited marked differences in distribution and habitat are also included. In the following comments the organisms appear in the order of their combined importance values for the four streams.

Peltoperla maria Needham (Plecoptera: Peltoperlidae) was the most important animal in three of the four watersheds; in the Old Field it ranked 26th. Greatest numbers of *P. maria* occurred in the Hardwood stream. *P. maria* contributed about 1/10 of the total biomass in the Hardwood stream and 1/20 of the total biomass in the Coppice stream. Although numbers were much lower than in the preceeding two streams, *P. maria* contributed about 1/20 of the biomass in the Pine stream. In the Old Field stream this insect comprised only 1/500 of the total biomass. This emphasizes the fact that the Pine and Old Field streams supported less *P. maria* biomass due to less hardwood leaf input. Peaks in abundance of *P. maria* were positively correlated with peaks in detritus input.

The Chironomidae had their greatest abundance in the Old Field. Few were collected in bare rocky areas. Species of Chironomidae collected included Diamesinae: *Diamesia nivoriunda* (Fitch); Chironominae: *Chironomus fulvipilus* (Rempel), *Zavralia* sp.; Tanypodinae: *Conchapelopia* sp.; *Orthocladius* sp., *Nanocladius* spp., *Pseudorthocladius* nr. *curtistylus* Goetghebuer, *Pseudorthocladius* sp. The chironomids are included collectively rather than separately because of the similarity of their feeding habits and the difficulty of sorting out individual species. *Conchapelopia* sp. was the only predator collected.

The larvae of *Optioservus immunis* Fall were next in importance. In the Red Cedar River, Elmidae larvae and adults were common on all bottom types and ranked second in importance for that study (Ball, et al., 1969). The adult elmid *Limnius latiusculus* Le Conte, ranked fifteenth in the four Coweeta streams combined. Adults of *O. immunis* were slightly less important.

Stenonema spp. were observed to feed on hardwood leaves which comprised most of the detritus in the Hardwood stream where they were most abundant.

Cambarus bartonii bartonii Fabricius (Decapoda) had its greatest importance in the Coppice stream. Crayfish accounted for about 1/2 of the biomass in the Old Field stream, 1/10 of the biomass in the Hardwood stream, 1/6 of the biomass in the Pine stream, and 1/3 in the Coppice stream where they were abundant in pools.

For *Ephemerella* spp. homogenity existed among the Pine, Old Field, and Coppice streams. According to Percival and Whitehead (1929) mosses and algae are the main food of this genus. The genus was least important in the heavily shaded Hardwood stream where very little moss and algae occurred. The most abundant species was *E. funeralis*.

Rhyacophila torva Hagen, *R. nigrita* Banks, *R. carolina* Banks, *R. minora* Banks, *R. glaberrima* Ulmer, and *R. fuscula* Walker were collected on the mats of moss which grew on rock outcrops in the streams. Ross (1944) observed that *Rhyacophila* fed upon chironomid larvae. While their seasonal abundance was not positively correlated with *Rhyacophila* in our samples, both had their greatest importance value in the Old Field stream. Studying the feeding habits of seven western North American species of *Rhyacophila*, Thut (1969) found that five were carnivores, one omnivorous, and one herbivorous. Chironomidae were the most numerous animals in the gut although Copepoda, Acari, and others were also important.

Paraleptophlebia sp. had its greatest importance in the Hardwood stream followed by the Pine and Coppice streams respectively. They were found in the habitat described by Day (1963): "They may be found in any part of the stream with a moderate or slow current but the preferred location is in slowly running shoal water 1/4 to 12 inches deep where the nymphs concentrate in deposits of decaying leaves, bark, and wood.

Diplectrona modesta Banks was reported by Ross (1944) to feed on plankton and sessil diatoms. Bacteria and fine detritus may also be a food source (Hynes 1970). In all watersheds except the Pine, the abundance of this filter feeder was inversely related to the amount of detritus collected. Filter feeders probably prefer areas of little detritus accumulation where they are exposed to optimum current.

Tipula had its greatest importance in the Coppice stream where it comprised about 1/3 of the total biomass. Specimens were principally found in leaf-filled pools at the bases of small waterfalls. In the laboratory they were observed to feed on deciduous leaves. Egglishaw and MacKay (1967) reported that densities of *Tipula* species were greatest in the pool areas of the streams they studied. This genus was responsible for about 1/10 of the biomass in the Hardwood and Pine streams and about 1/14 of the biomass in the Old Field stream. *Tipula abdominalis* (Say) and *Tipula ignoblis* Loew were collected.

The species *Eriocera longicornis* (Walker), *E. spinosa* (Osten Sacken) and *E. fultonensis* (Alexander) were collected. They were found in predominantly sandy areas of the streams. Gut analysis indicated that larger individuals were omnivores while the smaller ones were detritivores. The genus showed greatest numbers and biomass in the Old Field stream. Their distribution appears to be influenced somewhat by the abundance of a sandy substrate but feeding relationships may be the determining factor. More work is needed on the feeding habits of this genus.

The abundance of the filter feeder *Parapsyche cardis* Ross, like *D. modesta* was inversely related to amounts of detritus. *P. cardis* was more important in the Coppice stream than in the other streams. Although the discharges of the four Coweeta streams were similar the abundance of small waterfalls in the Coppice stream made available more suitable habitats than were present in the other streams. These waterfalls produced increased currents and Edington (1968) has shown that caddis larvae constructed their nets in currents where they are most efficient. *P. cardis* was least important in the Pine stream which also had the lowest discharge.

The importance value of the predator *Lanthus albistylus* Hagen was much greater in the Pine stream than the other three streams.

Isogenus (*Yugus*) *bulbosus* Frison was most important in the Coppice and Hardwood streams where it possibly fed on insects and/or deciduous leaves which collected on debris and in the pools. According to Richardson and Gaufin (1971) *Isogenus elongatus* Hagen is usually carnivorous but under certain conditions exists entirely on detritus. They found the diet to be 64.9% animal material and 31.2% plant material.

The salamander species *Desmognathus ochrophaeus* Cope, *D. fuscus* Green, *D. monticola* Dunn and *D. quadramaculatus* Holbrook were found in the 4 streams. Gut analysis revealed that they are predaceous on all other animals in these streams. The Hardwood stream supported the greatest salamander biomass (Table 14) and the Coppice stream, although it supported the greatest animal biomass, had the lowest biomass of salamanders. It is hoped that more detailed gut analyses will help explain this situation.

Although their importance values were small the four following insects should be included in the discussion due to their abundance in the Old Field stream. *Anchytarus bicolor* (Melsh.) (Ptilodactylidae: Coleoptera) was most abundant in shallow samples containing much grass and grass roots. According to Leech and Chandler (1963) their staple diet consists of roots of grasses and leaf mold. Grasses were more dense in the channel of the Old Field stream than in any of the other streams.

Another insect showing a peculiar distribution in the Old Field stream was *Ochrotrichia* sp. (Trichoptera: Hydroptilidae). Collections were usually recorded from moss covered granite outcrops. Pervical and Whitehead (1929) collected more hydroptilids from moss on stones than on other substances and reported their food to be algae and diatoms. Hughes (1966) found that hydroptilids were more abundant in open areas of streams than shaded areas. He also stated that Trichoptera were often limited by availability of case making materials. Bank cutting and channel degradation in the Old Field stream could have provided a greater amount of suitable sand grains than was available in the other streams. The moss outcrops however are suspected to be the central factor influencing the distribution of *Ochrotrichia*. Nielsen (1948) reported that larval mouthparts of hydroptilids are modified for piercing and sucking the cells of filamentous algae or scooping up diatoms.

A small Chironomidae, Zavralia sp., was collected most frequently in the Old Field stream. It built a minute case about 5mm long and similar to cases of the caddis fly family Odontoceridae. Its distribution may have been influenced by the availability of suitable sized grains of sand for its case.

The distribution of the water penny, Ectopria sp., seems to be affected by the amount of sunlight reaching the stream. According to the Duncan's test the numbers of Ectopria in the Old Field were significantly greater than in the other streams. This organism was least important in the heavily shaded Hardwood stream. In the Old Field stream they were most frequently collected on algae covered stones. Pennak (1953) reports that algae are the chief food of this genus.

Summary and Conclusions

All Coweeta streams and low concentrations of dissolved substances and were similar chemically (Table 10). Due to low temperatures all streams had high dissolved oxygen.

The vegetation on each watershed is probably the main factor affecting species composition in the streams although flow rate, gradient, and substrate also influence distribution. Allochthonous detritus was the main source of energy for the primary consumers since there were sparse aquatic macrophytes and probably little aquatic primary production.

Most of the differences in the fauna of the four watersheds can be explained by the availability of food and/or case-making materials, both of which are directly or indirectly controlled by vegetation. The biomass/unit area in Coweeta streams agrees with results from several other aquatic environments (MacKay and Kaliff, 1969) although our numbers were lower.

Most genera occurred in all four streams but their importance varied from stream to stream. The results of Duncan's test performed on total numbers of individuals in each insect category showed that among streams the Old Field stream was least like the other three. The most important organism was *Peltoperla maria* followed by Chironomidae, *Diplectrona modesta*, and *Tipula* spp. As would be expected, most of the important animals were herbivores and only a few such as *Lanthus* and *Desmognathus* were carnivores. The standing crops of detritivores increased and decreased at roughly the same times as did detritus. Filter feeders such as *Diplectrona* and *Parapsyche* showed an inverse relation to detritus.

Although it was not quantified in this study the influence of fine detritus upon insect distribution should not be overlooked. Fine detritus and its associated fungal and bacterial community is probably essential to the diets of many smaller organisms such as the Elmidae, some Chironomidae and some filter feeders (Hynes 1970). Amounts of fine detritus upon insect distribution should not be overlooked.

Fine detritus and its associated fungal and bacterial community is probably essential to the diets of many smaller organisms such as the Elmidae, some Chironomidae and some filter feeders (Hynes 1970). Amounts of fine detritus in the water is controlled more by detritivores than by stream flow. Kilmer and Cummins (1971) estimate that only 5% of leached large particulate organic matter is broken into fine detritus by the stream's mechanical action.

Several workers have reported low diversity and total numbers in streams flowing through land devoid of deciduous trees (Minshall, 1968, and Egglishaw and MacKay, 1967). This was not the case in the Old Field stream where we found high numbers of individuals and species. Although some detritus feeders such as *Peltoperla maria* were unimportant in the Old Field stream others such as *Cambarus b. bartoni* were abundant. Perhaps the prolific input of grass detritus into this stream was utilized by crayfish in lieu of the hardwood leaf detritus of the other streams. Slightly higher water temperatures caused by clear cutting could also have influenced the abundance of organisms in this stream (Swift and Messer, 1971).

The abundance of *Rhododendron* leaves may explain why the Hardwood stream supported only about 1/3 as much animal biomass as the Coppice stream. Both streams had about the same amount of leaf detritus but the proportion of *Rhododendron* leaves was much less in the Coppice stream. Wallace, et al. (1970) have shown that *Rhododendron* leaves were not a preferred food of an herbivorous stonefly. *Rhododendron* leaves appeared resistant to decay and subject to little feeding by invertebrates since intact leaves were found throughout the year.

The Pine stream supported only 1/5 to about 1/2 as much animal biomass as the other streams. In laboratory experiments (Wallace, et al., 1970) pine needles were not a preferred food of *Peltoperla* nymphs. About 1/2 of the detritus in the Fine stream was pine needles and the rest was contributed by littoral hardwood growth, much of which was *Rhododendron*. The scarcity of palatible detritus partially explains the lower number of insects there. These results indicate that forest monoculture practices involving pine watersheds may seriously effect secondary production of aquatic invertebrates.

The Coppice stream had from two to five times as much animal biomass as the other streams. This was probably due to its larger drainage basin and the composition of leaf detritus which contained less *Rhododendron* than the Hardwood stream. The greater number of small detritus filled pools in the Coppice stream resulted in more extensive favorable hatitats for *Tipula*, *Peltoperla* and *Cambarus*. Above these pools were small waterfalls where *Parapsyche* occurred in the swift current.

Table 9. Physical Features of Four Streams at the Coweeta Hydrologic Laboratory.

Watershed	Old Field	Hardwood	White Pine	Coppice
Area (ha)	9.1	12.8	13.9	16.6
Elevation (m)	700-900	727-990	734-1014	717-900
Mean annual discharge (cu.ft./mi^2)	2.60	2.79	2.04	2.69
Temperature (C)				
maximum (August)	18.5	17.5	16.0	16.0
minimum (December)	5.5	2.0	2.0	5.2
Turbidity (jackson units)				
maximum	26	12	12	20
minimum	1	0	0	6
Dissolved oxygen (ppm)				
maximum	10.0	13.8	12.0	10.0
minimum	8.0	8.0	8.8	7.2

Table 10. Chemical Features of Four Streams at the Coweeta Hydrologic Laboratory.

Watershed	Old Field	Hardwood	White Pine	Coppice
Conductivity (mmho)				
max	17.6	14.0	11.0	10.3
min	12.0	11.2	10.5	8.7
Alkalinity (ppm)	10.0	10.0	10.0	10.0
pH	6.7	6.8	6.9	6.7
Total phosphate (ug/l)	9.84	7.49	7.39	4.05
Ca (ppm)*	1.077	.649	.516	.470
Mg (ppm)*	.648	.289	.213	.252
K (ppm)*	.616	.480	.446	.431
Na (ppm)*	1.125	.913	.763	.639

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* Swank and Elwood, 1971

Table 11. Maxima, minima and monthly averages (g/m^2) of detritus removed from Coweeta streams.

Watershed	Old Field	Hardwood	White Pine	Coppice
maximum	172.2 (Feb.)	223.7 (Nov.)	117.3 (Sept.)	262.0 (Nov.)
minimum	21.6 (Jun.)	34.9 (Jul.)	37.5 (Jun.)	11.9 (Apr.)
average	74.6	110.2	70.9	109.9

Table 12. Rank by relative importance of benthic organisms collected from Coweeta watersheds from August 1968 to July 1969. Adult forms are marked (A).

Organism	Old Field	Hardwood	Pine	Coppice
Collembola	35	20	12	26
Ephemeroptera				
Ephemera sp.	53	--	--	--
Stenonema spp.	18	7	8	11
Eperous sp.	25	27	25	25
Isonychia sp.	29	49	38	46
Paraleptophlebia sp.	20	6	13	15
Ephemerella spp.	7	28	5	10
Baetis sp.	16	40	19	18
Odonata				
Cordulegaster erroneus Hagen	50	31	30	48
Lanthus albistylus Hagen	11	19	3	9
Plecoptera				
Peltoperla maria Needham	26	1	1	1
Nemoura sp.	17	26	35	17
Leuctra sp.	38	29	20	29
Acroneuria arida Hagen	46	23	24	31
Isogenus (*Yugus*) *bulbsosus* Frison	28	5	17	5
Alloperla sp.	37	17	18	13
Coleoptera				
Promoresia tardella Fall (A)	53	--	--	48
P. tardella Fall	52	--	--	--
Limnius latiusculus Le Conte (A)	8	12	14	28
L. latiusculus Le Conte	22	36	23	32
Optioservus immunis Fall (A)	9	16	27	35
O. immunis Fall	3	9	2	30
Ectopria sp.	13	38	21	21
Anchytarsus bicolor (Melsh.)	10	39	26	48

Table 12. (Continued)

Organism	Old Field	Hardwood	Pine	Coppice
Trichoptera				
Rhyacophila spp.	5	14	15	19
Chimarra sp.	54	--	47	49
Sortosa sp.	--	52	53	--
Wormaldia sp.	27	33	43	27
Lype diversa (Banks)	30	13	22	33
Polycentropus sp.	--	52	--	--
Diplectrona modesta	4	3	6	4
Parapsyche cardis Ross	14	10	9	7
Ochrotrichia sp.	21	--	--	47
Pycnopsyche guttifer (Walker) and *P. sabripennis* (Rambur)	31	25	36	20
Pycnopsyche gentilis (McLachlan)	51	43	53	--
Neophylax sp.	23	41	37	14
Oecetis sp.	--	--	53	40
Lepidostoma sp.	34	37	31	48
Pseudogoera singularis Carpenter	32	34	40	22
Sericostoma pele Ross	44	18	28	37
Diptera				
Tipula spp.	6	11	7	2
Eriocera spp.	1	8	11	3
Pedicia sp.	39	24	33	23
Geronomyia sp.	51	52	50	--
Antocha saxicola O.S.	53	35	32	40
Limnophila sp.	51	52	51	47
Dicranota sp.	40	22	34	24
Pseudolimnophila sp.	36	50	42	--
Unidentified Tipulid species	48	4	48	39
Protoplasa fitchii (O.S.)	53	53	--	--
Blephariceridae	57	51	53	--
Psychodidae	51	52	51	47
Telmatoscopus sp.	49	53	41	43
Dixa sp.	43	44	49	36
Simulium sp.	24	48	52	44
Chironomidae	2	2	4	6

Table 12. (Continued)

Organism	Old Field	Hardwood	Pine	Coppice
Diptera				
Zavralia sp.	33	52	--	47
Ceratopogonidae	19	30	29	16
Tabanus sp.	53	--	--	--
Dolichopodidae	--	42	46	49
Empidae	41	50	44	45
Chelifera sp.	53	45	53	42
Non-Insects				
Annelida	49	32	39	34
Decapoda	12	21	10	8
Desmognathus spp.	15	15	16	12
Eurycea bislineata wilderae Dunn	47	--	--	38

Table 13. Results of Duncan's test on total number of organisms collected to the right of each species and the one at the top of the column. O = Old Field, H = Hardwood P = Hardwood, P = Pine, C = Coppice.

	O	H	P	C
Podura aquatica	C	P,C	H	O,H
Baetis sp.	C	P	H	O
Ephemerella sp.	P,C	"no others"	O,C	P,O
Paraleptophlebia sp.	P,C	"	O,C	P,O
Stenonema sp.	C	"	O,C	P,O
Peltoperla maria	"no others"	P,C	H,C	H,P
Nemoura sp.	H	O,H,P	H,C	H,P
Leuctra sp.	H,C	O,H,P	H,C	O,H,P
Optioservus immunis (Adult)	"no others"	C	"no others"	H
Optioservus immunis (Larvae)	"	C	"	H
Liminus latiusculus (Adult)	"	H,C	H	H
Ectopria spp.	"	P,C	H,C	H,P
Anchytarus bicolor	"	P,C	H,C	H,P
Ochrotrichia sp.	"	"	"	"
Parapsyche cardis	"	"	"	"
Diplectrona modesta	H	O	C	P
Sericostoma pele	P,C	"no others"	O,C	O,P
Rhyacophila	H,C	O,P,C	H,C	O,H,P
Tipula spp.	H,P	O,P	O,H	"no others"
Ceratopogonidae	H	O,P,C	H,C	H,P
Chironomidae	"no others"	P,C	H	H

Table 14. Average monthly standing crops/m^2 and ash free dry wt./m^2 for four streams, Coweeta Hydrologic Lab, Macon Co., N.C.

	Old Field		Hardwood		Pine		Coppice	
	Numbers	Grams	Numbers	Grams	Numbers	Grams	Numbers	Grams
Cambarus	4.6	.788	2.0	.104	4.2	.100	3.2	1.110
Ephemerella	71.6	.029	10.1	.002	43.0	.009	38.6	.008
Stenonema	8.7	.010	37.2	.021	19.4	.016	13.0	.015
Lanthus	7.4	.130	3.4	.029	11.0	.056	6.5	.042
Peltoperla	3.5	.004	151.1	.104	108.4	.031	143.8	.155
Isogenus	9.4	.002	18.2	.058	20.4	.002	41.4	.025
Paraleptophlebia	23.8	.002	92.5	.009	25.2	.005	22.1	.004
Rhyacophila	22.4	.011	15.6	.016	11.5	.006	20.6	.002
Parapsyche	11.3	.030	6.1	.107	19.1	.014	17.2	.044
Diplectrona	104.6	.052	88.5	.066	24.6	.017	81.5	.027
Optioservus (larva)	167.00	.033	2.7	.001	71.5	.014	6.6	.001
Limnius (adult)	71.6	.007	23.1	.002	35.2	.004	8.6	.001
Tipula	8.5	.128	3.9	.117	3.3	.058	24.0	1.080
Eriocera	82.3	.037	49.6	.015	20.7	.015	40.1	.020
Chironomidae	218.7	.002	93.8	.007	64.7	.008	109.3	.010
Desmognathus	4.9	.195	4.2	.347	4.4	.177	5.9	.104
Total of top 16	820.3	1.460	602.0	1.005	486.6	.532	582.4	2.648
Total of all others	394.0	.177	202.3	.066	229.7	.056	200.7	.100
Combined total	1214.3	1.637	804.3	1.071	716.3	.588	783.1	2.748

SECTION IX

MINERAL STUDIES

From the foregoing discussion it is evident that the stream subsystem model of most small watersheds is supported primarily by the detritus imput from the surrounding watershed, especially autumn shed leaf material. Since most nutrient losses from such watersheds are via the stream it is desireable to know the nutrient content of stream organisms as well as the role they play in stream nutrient cycling, especially since the trophic activities of detritus feeding arthropods and their predators are involved in the distribution and transfer of nutrients during the decomposition processes (Reichle et al. 1969).

W. R. Woodall undertook a study at Coweeta Hydrologic Laboratory in an attempt to get initial data in the following areas: (1) Determination of nutrient enrichment of water due to leaf decomposition and insect feeding. (2) Determination of whole-body and standing crop concentrations of calcium, potassium and magnesium in major benthic fauna of four Coweeta streams.

A Nutrient Enrichment of Water Due to Insect Feeding

Materials and Methods

Nymphs of the stonefly *Peltoperla maria* Needham (Plecoptera: Peltoperlidae) were collected from Coweeta streams and kept in the laboratory in creek water at 12 C. Senescent alder leaves (*Alnus serrulata* L.) were shaken from a streamside tree in late October just prior to natural abscission. The leaves were washed and leached in flowing tap water for two weeks. They were then air dried and cut in half, removing the petiole. Each half was weighed and placed in a container designated as experimental or control. The containers were 15 cm plastic boxes. Two hundred ml of creek water in each container covered the leaves. Thirty pairs of containers were set up. After the leaves had soaked for 24 hours to ensure complete wetting, five to seven *Peltoperla* nymphs were placed in each experimental container. Pierced tops were placed on the boxes and both experimental and control containers were incubated at 12 C.

After an initial 12 day period, 5 experimental and 5 control containers were removed from incubation at approximately weekly intervals for 6 weeks. The leaves were air dried and reweighed to determine weight loss. One or two 12 mm diameter discs were cut from each leaf half with a #9 cork borer. Leaf tissue (other than the discs) and the water from each container were analyzed by atomic absorption to determine concentrations of calcium, potassium, magnesium and sodium.

The discs were attached to stubs and gold coated for examination by scanning electron microscopy. Several fields on each stub were examined and photographed at magnifications of 20x, 100x, 1000x and occasionally 200x, 500x, or 5000x. Leaves were examined from the second and seventh weeks of incubation. Six pairs of control and experimental leaf halves as well as three *Peltoperla* and two frass samples were examined.

Alder was selected as the experimental leaf because it is abundant along streams, it is readily eaten by *Peltoperla* (Wallace *et al.* 1970), and because aquatic hyphomycetes were reported to grow on alder leaves in streams (Ingold 1942). *Peltoperla* was selected as the experimental animal because it was the most abundant detritivore in Coweeta streams.

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Results and Discussion

Calcium concentrations were significantly higher in experimental water containing insects and leaves than in control water containing only leaves. The amount of calcium lost to the water in control containers was positively correlated with the amount of leaf material leached (Figure 11). In the experimental containers, the relationship was not as close. (This is probably because some calcium was retained by the insect). Calcium increased more in the water than did other elements (Table 15). Results of a similar experiment are included for comparison (Table 16). This cation is found in plant cell walls where it reacts with pectic acid to form relatively insoluble salts in the middle lamella. Inside vacuoles, calcium precipitates as crystals of calcium oxylate and also forms insoluble salts in other ways (Salisbury and Ross 1969). It is reasonable to believe that most calcium would be released to the water after the leaf was digested.

Concentrations of potassium were lower in control containers than in fresh creek water. This was also true in another experiment in which *Pteronarcys scotti*, another stonefly, was fed alder leaves (Table 16). In the present study, concentrations of potassium in water were inversely related to the amount of leaf leached or eaten (Figure 12). It appeared that leaves absorbed or absorbed potassium from the water. Since dead leaves are readily leached of potassium (Carlisle *et al*. 1966, Cromack 1972), most of the potassium probably leached from the leaf during the preleaching period.

Magnesium also showed a significant increase in experimental containers. The concentration of magnesium continued to increase in *Peltoperla* experimental containers after organic leaching had stabilized (Figure 13). Since the magnesium ion is bound in the center of the chlorophyll molecule (Salisbury and Ross 1969), digestion probably plays a major role in the release of this element into the water.

Sodium was slightly more concentrated in water in experimental containers than in controls (Table 15). The concentration of sodium in water was .7-.8 ppm and did not increase, regardless of the amount of leaf material leached (Figure 14) and appeared to be in osmotic equilibrium. The role of sodium in plants and invertebrates is not well understood.

Water collected at Coweeta in October had a higher concentration of calcium, potassium, magnesium and sodium than water collected in January. This was undoubtedly due to leaching of freshly fallen leaves. Concentrations of potassium were 2 fold higher in October than in January. Concentrations of the other three cations were less than 50% higher in October than in January. Long term release of chemically bound ions such as calcium and magnesium seems to be facilitated by detritivore feeding.

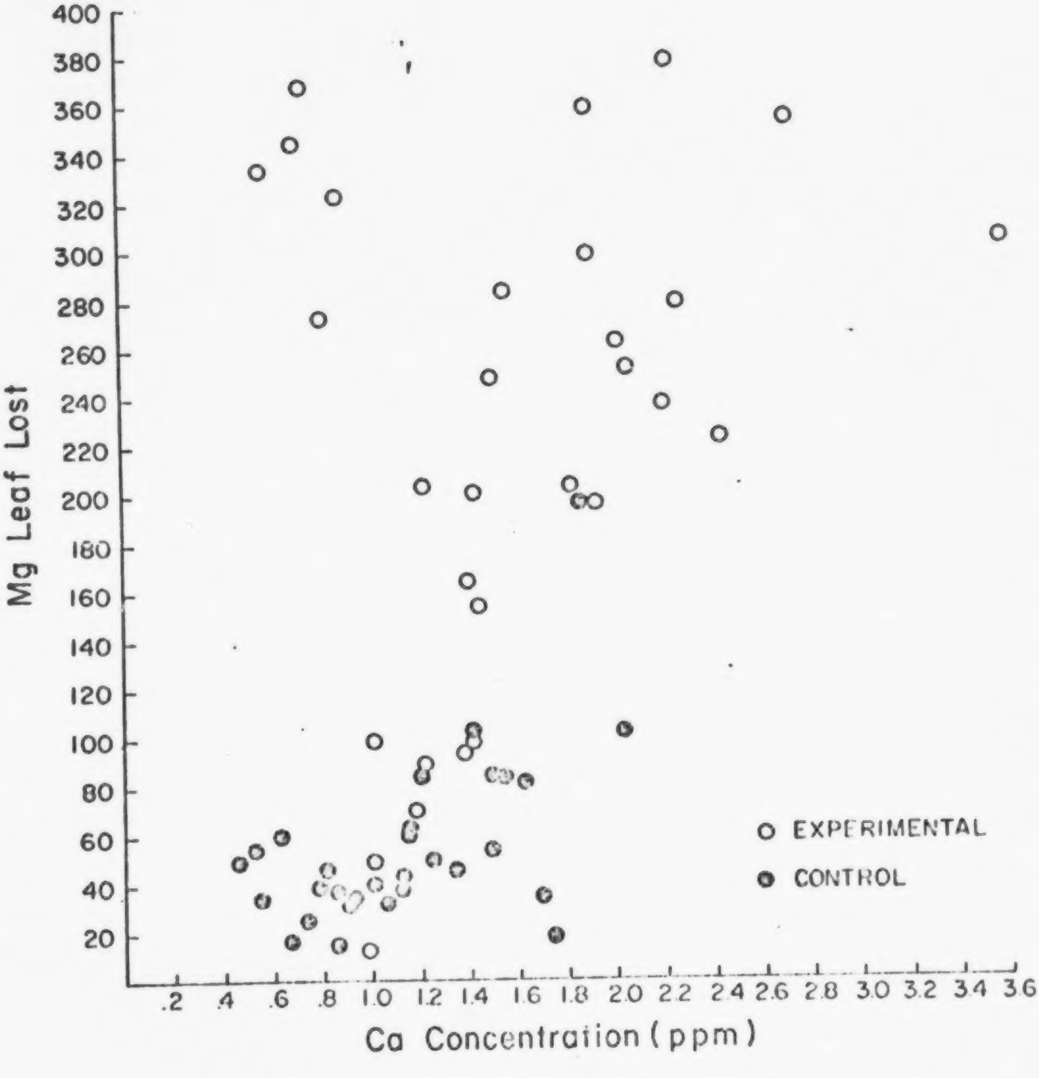

Figure 11. Relationship between amount of leaf lost through eating and/or leaching and concentration of calcium in the water.

Table 15 . Nutrient concentrations (ppm) in water after 12 - 46 days of feeding by *Peltoperla* nymphs.

	Potassium	Sodium	Calcium	Magnesium
Untreated creek water T= 0 days	.381	.631	.562	.268
Experimental containers T= 12-46 days	.504	.744	1.596	.489
Control containers T= 12-46 days	.364	.733	1.068	.332

Table 16 . Nutrient concentrations (ppm) in water after 6 weeks of *Pteronarcys* feeding.

	Potassium	Sodium	Calcium	Magnesium
Untreated creek water T= 0 days	.755	.889	.781	.334
Untreated creek water T= 6 wks	.733	.855	.744	.332
Experimental containers T= 6 wks	.752	1.322	2.005	.431
Control containers T= 6 wks	.661	1.037	1.142	.289

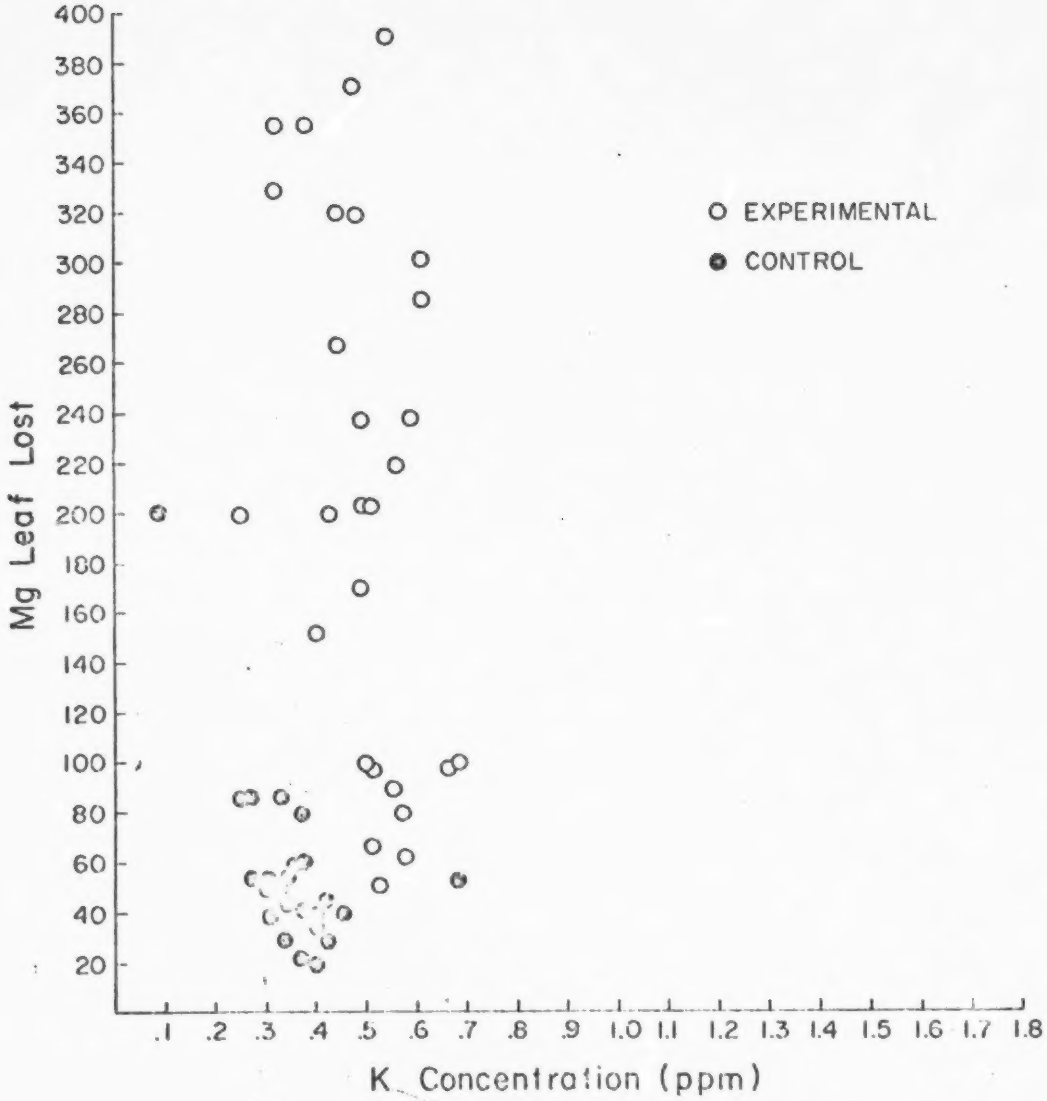

Figure 12 . Relationship between amount of leaf lost through eating and/or leaching and concentration of potassium in water.

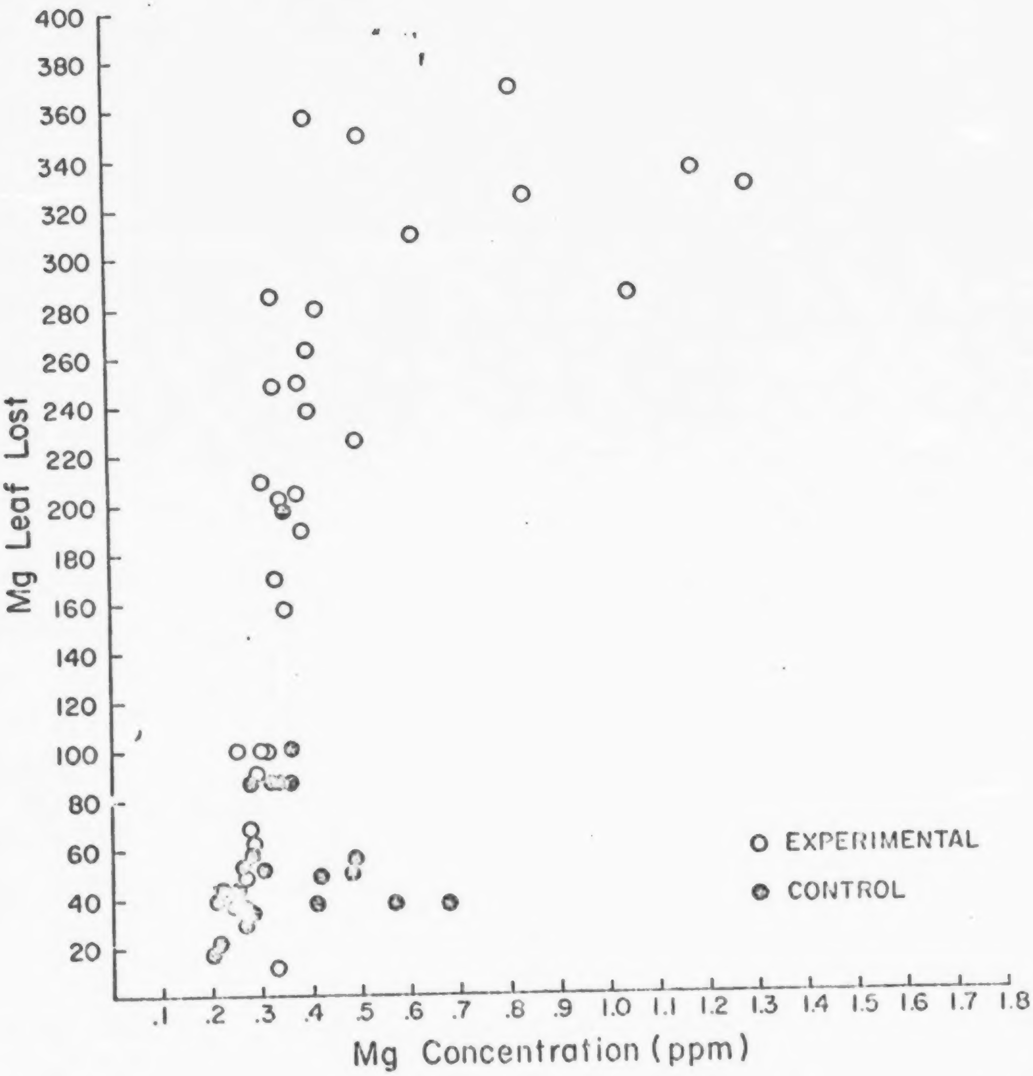

Figure 13. Relationship between amount of leaf lost through eating and/or leaching and concentration of magnesium in water.

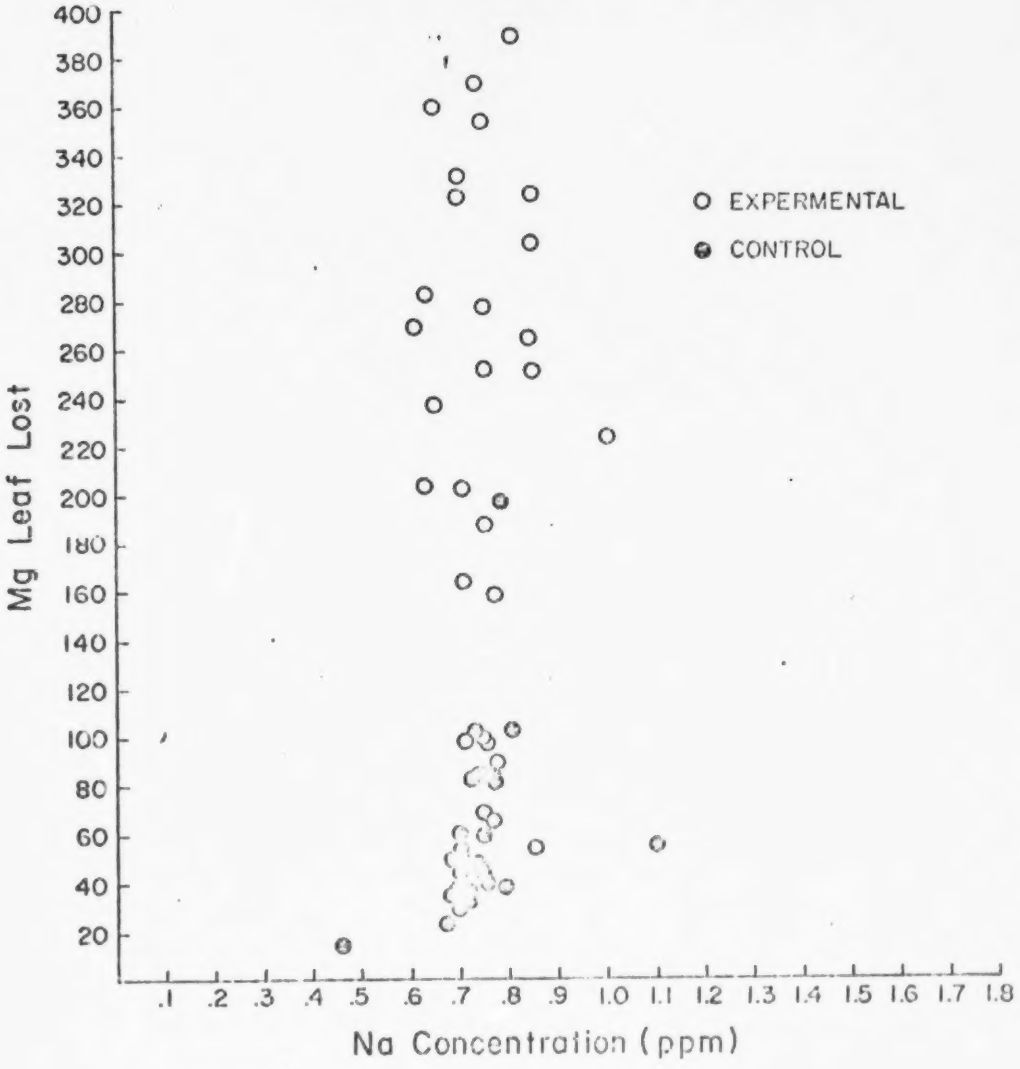

Figure 14 . Relationship between amount of leaf lost through eating and/or leaching and concentration of sodium in water.

Results of Electron Microscope Examination of Leaf Discs from Experimental Feeding Studies

Ingold (1942) reported that fungal hyphae (aquatic hyphomycetes) develop within four weeks after leaves are submerged in streams. In the present study, fungi were not abundant on control of experimental leaves at the beginning (12 days) or the end (46 days) of the incubation period. Only two leaf halves had recognizable fungus on the surface. These were both halves of the same leaf which were removed at 12 days. The control had two colonies of Myxomycetales (slime mold) and one cluster (fruiting body) was observed on the experimental leaf half. A few structures that appeared to be fungal hyphae were seen growing from the stomata but these were not common. No fungi were observed on the mouth or anus or any other part of the stonefly's body. Neither were fungi seen in the frass.

In an attempt to culture stream fungi, sterile seeds were incubated in flasks of Coweeta creek water at 12 C and 25 C for 7 days. *Peltoperla* frass from experimental containers was plated onto Czapeks, V8 and potatoe dextrose agar and incubated at 12 C and 25 C for 10 days. Both attempts to culture fungi were unsuccessful. Some bacteria developed on the agar, however.

Three clusters of *Phylactinia* (Ascomycetales: Eryciphaceae), a powdery mildew, were seen on a leaf which had been leached for two weeks in tap water but not incubated. None of these were seen on the incubated material.

The most common microflora present was a filamentous bacterium in the family Actinoplanaceae of the order Actinomycetales. It is similar to the genus *Actinoplanes* which was described by Couch (1949) as follows:

> A mycelium of delicate, non-septate hyphae .3-.8 u thick without aerial mycelium...but producing spores singly on the distal ends of short lateral branches of the vegetal mycelium.

The filaments were present on control leaves as well as uneaten portions of experimental leaves. Although it was impractical to quantify the number of filaments by electron microscopy, they appeared to be more abundant on control leaves and showed no difference in abundance between 12 and 46 days.

Peltoperla seemed to be feeding indescriminately on the leaves and not selectively on the mycelia. Certain areas of the leaf were eaten away layer by layer, from the waxy cuticle to the mesophyll layer. No Actinoplanes mycelia were seen in areas of intense feeding and it is probable that they were eaten with the leaf surface. In control leaves, mycelia could be seen on the waxy cuticle.

A film was seen on the trichomes of all leaves. It was more abundant on the controls than on experimental leaves. The material showed no signs of cellular structure, even at 1000 to 5000x and was presumed to be a bacterial secretion.

There was not enough fungus present to be a significant food source of Peltoperla and it is doubtful that the bacterial growth was dense enough to contribute much to the stoneflies' diet. The most striking difference between the control and experimental containers was the reduction of the above mentioned film on the experimental leaf halves. It was possibly mechanically removed by the insects' normal activity or eaten by the insects.

SECTION X

DETERMINATION OF WHOLE-BODY AND STANDING CROP CALCIUM, POTASSIUM AND MAGNESIUM IN FOUR COWEETA STREAMS

Materials and Methods

Samples were collected as described previously (Section VIII) and maintained on ice, and processed within 24 hours after returning to the laboratory. Samples were dried at 105 C for 24 hours and dessicated over $CaCl_2$ at least 24 hours to insure constant weight. Densities were determined from quantitative samples, however additional qualitative samples were necessary in order to obtain enough organisms for analysis.

Mineral Analyses

Analytical glassware was washed once in 70% reagent grade HCl overnight, rinsed 6 times in tapwater followed by 6 rinses in deionized water. After the original washing, 10% reagent grade HCl was used for subsequent washing. Thirty ml Pyrex beakers were used for all except the largest samples.

Samples and beakers were dried separately overnight at 75 C. They were cooled in a desiccator over $CaCl_2$ for 15 minutes prior to weighing. Weights were obtained on a 4-placed Mettler balance. Beakers were weighed, the sample was added and the beakers reweighed. Substraction yielded the weight of the sample.

Acid digestion of samples was accomplished as follows: Approximately 5 ml of concentrated HNO_3 was added to the beaker which was covered with a watch glass and then buried about 1/2 inch in a sand bath. The sand bath was gradually heated to 190-200 C on a Corning PC-35 hot plate. The sample was evaporated to dryness and the sides of the beaker flushed with 2 ml concentrated HNO_3. This was repeated until no fumes could be detected coming from the beaker. Then 5 ml concentrated HNO_3 was added and the sample was evaporated a final time.

When all organic material had been driven off, the ash was redissolved in 1 ml concentrated reagent grade HCl and then flushed with deionized water into a 100 ml volumetric flask with cap. Samples were refrigerated until they could be analyzed by atomic absorption.

The samples were analyzed on a Bausch and Lomb atomic absorption spectrophotometer, model AC220. Samples were burned in a mixture of acetylene and breathing air. One percent lanthanum chloride was added to the samples and blanks for magnesium and calcium analysis to supress interference of phosphate and sulfate ions.

Sixteen groups of organisms were included in this discussion. All other organisms in the streams comprised less than 6% of the total biomass.

Each of the four Coweeta streams were divided into a generalized five compartment model (Figure 15). The true picture is much more complicated than this, however since current techniques and available personnel would have made data gathering almost impossible with the personnel and equipment available only the 5 compartments in Table 19 were utilized. Primary producers were put into two compartments, detritus and periphyton. As was stated previously, many investigators feel that fungus and bacteria play a major role in detritus breakdown. Some have advocated the inclusion of microflora as subcompartments within the detritus compartment (Hynes 1970, Kilmer and Cummins 1971). Since microflora seemed to be of only minor importance in experimentally manipulated leaves, they were not included as part of this model. This is not intended in anyway to preclude its possible importance.

The consumers were divided into three major compartments which were detritivores, grazers and predators. Organisms were assigned to these compartments based on gut analyses and the literature. If an organism's diet consisted of various amounts of detritus, periphyton and/or other animals, its standing crop was apportioned among the compartments based on the relative amounts of the different food types eaten.

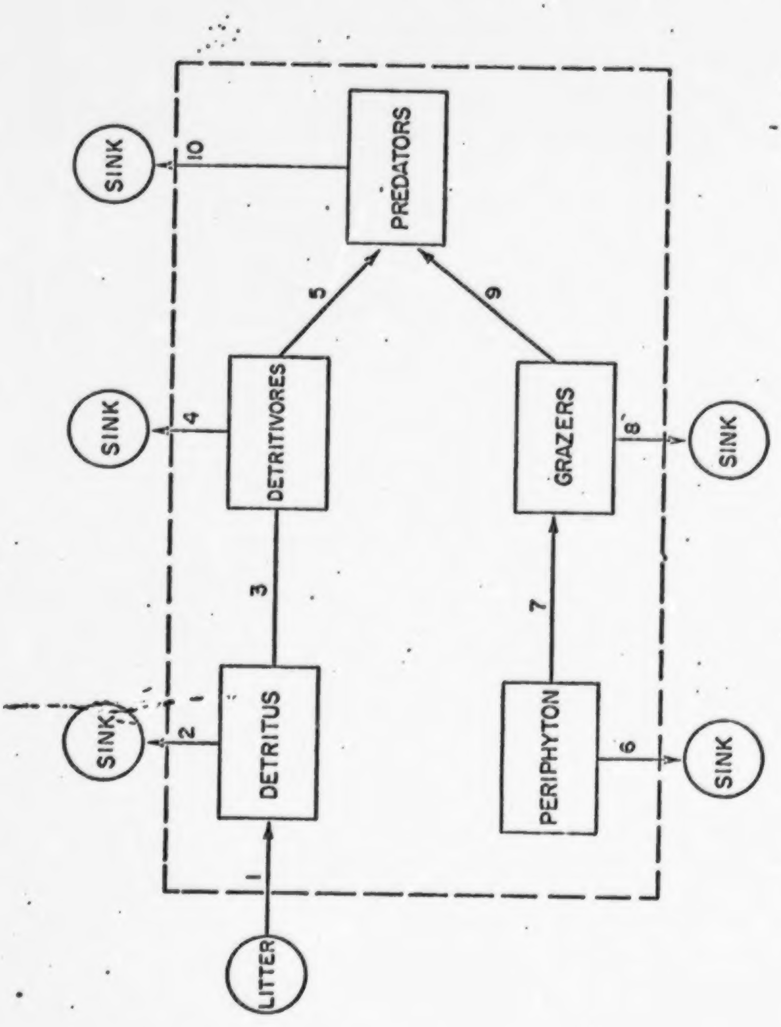

Figure 15. General food web diagram of a small Southern Appalachian stream.

Results and Discussion

Table 17 lists the mineral concentrations of the top 16 taxa representing 96% of the biomass in the four Coweeta streams studied. Crayfish (Cambarus) and salamanders should be especially noted since the calcium concentrations of these two were much much higher than any other organisms due to the calcium carbonate in the exoskeleton of the crayfish and calcium in the bone structure of the salamanders (again salamanders are the dominant predators in these small streams since no fish are present). These two taxon probably represent real "sinks" in the calcium movement through this system since the waters of the Coweeta streams represent some of the softest waters in the world (less than 10 ppm methyl orange). No molluscs are present in the streams.

Table 18 presents the average dry wts. based on monthly samples, and Appen. Table I the average seasonal numbers per m^2.

Quarterly standing crops of detritus biomass and the animal biomass by trophic level is presented in Table 19. Again, if any of the top 16 taxons food based on gut analysis was found to consist of varying amounts of detritus, periphyton and/or other animals it was apportioned among the compartments based on relative amounts of food present in the gut.

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Table 17. Nutrient concentrations (ppm) in major taxa.

Taxon	Calcium	Potassium	Magnesium
Cambarus	100300	1900	2263
Ephemerella	7700	2300	2936
Stenonema	3800	1900	1949
Paraleptophlebia	8700	1900	4480
Lanthus	1700	4800	1225
Peltoperla	3500	1800	1649
Isogenus	3900	1700	1181
Elmidae (Adult)	4200	1300	1439
Elmidae (Larvae)	3700	2000	2374
Rhyacophila	7900	1700	2005
Diplectrona	3500	2700	1395
Parapsyche	3000	1900	1177
Chironomidae	7900	2100	3253
Tipula	4300	7300	2317
Eriocera	3800	7100	2010
Desmognathus	39300	2300	2179

Table 18. Average dry weights (mg/individual) based on monthly samples.

Taxon	Summer	Fall	Winter	Spring
Cambarus	722.55	53.5	1135	206.43
Ephemerella	1.19	.41	.68	.96
Stenonema	7.58	2.15	3.9	3.52
Paraleptophlebia	.76	.7	.7	.68
Lanthus	3.49	5.52	9.15	8.53
Peltoperla	1.97	2.48	3.15	3.94
Isogenus	2.01	2.83	2.2	11.63
Elmidae (Adult)	.8	.27	.34	.42
Elmidae (Larvae)	.2	.13	.12	.2
Rhyacophila	1.3	.52	.55	.58
Diplectrona	1.68	1.26	1.21	1.18
Parapsyche	5.3	3.6	3.62	4.82
Chironomidae		.12	.11	.28
Tipula	97.3	7.96	21.22	46.79
Eriocera	3.66	1.42	1.28	2.41
Desmognathus	97.04	62.94	112.75	58.86

Table 19. Seasonal standing crop biomass (mg/m^2) for each trophic level (1971-72). Values are means of monthly samples. * = detritivores without crayfish; ** = predators without salamanders.

Watershed	Trophic level	Summer	Fall	Winter	Spring
Old field	Detritus	34030	34020	136900	79870
	Detritivores	9529.02	358.5	6156	2273.89
	Detritivores*	1075.18	358.5	481	766.95
	Glazers	34.77	60.48	93.68	200.03
	Predators	344.51	655.39	700.11	812.76
	Predators**	247.47	151.87	170.18	518.46
Hardwood	Detritus	54640	152960	145520	101930
	Detritivores	3270.14	835.02	4013.11	2262.07
	Detritivores*	596.7	701.27	948.61	1704.71
	Grazers	61.05	65.11	63.51	74.02
	Predators	516.99	349.67	622.24	588.23
	Predators**	157.94	192.32	137.41	276.27
Pine	Detritus	65140.	71270	67180	80140
	Detritivores	5092.44	600.42	6553.97	1967.14
	Detritivores*	540.37	332.9	538.47	1141.42
	Grazers	32.12	32.91	59.25	62.25
	Predators	668.1	861.78	546.8	623.69
	Predators**	212.01	159.44	208.55	488.31
Coppice	Detritus	50950	216200	158450	49250
	Detritivores	3520.73	1120.4	8581.44	1148.56
	Detritivores*	413.76	1120.4	2565.94	673.77
	Grazers	77.72	78	85.88	62.61
	Predators	734.35	591.19	1702.6	542.45
	Predators**	278.26	245.02	428.53	483.59

COMPARTMENTS

Kilmer and Cummins (1971) estimated that about 20 percent of leaf weight is lost through leaching. Cromack (1972) has shown, in leaching experiments using leaves from seven species of hardwoods, that from 5 to 26 percent of leaf weight is leached by the end of five days in water. We have found that even after a ten day leaching period, alder leaves loose an additional 2 to 8 percent in an ensuing four to six weeks in water. The rates of mineral leaching in leaves vary greatly from the rate of biomass loss. Potassium leaches almost immediately upon contact with water, but almost no calcium and magnesium leaching occurs. Cromack's leaching experiments showed that hardwood leaves were less than .01 percent potassium after they had leached for five days in a stream. Original concentrations were as high as .96 percent potassium. Our own work showed that potassium may comprise as much as .1 percent of leaf weight in alder leaves after 52 days. Alder leaves, and possibly others, appeared to be so depleated of potassium after leaching for ten days in a flowing system, that they absorbed potassium from the water in experimental containers.

Alder leaves were found to be about 1 percent calcium. This was supported by Cromack's data for hardwood leaves which ranged from .4 to 2.3 percent calcium. Alder leaves leached for up to 52 days and Cromack's leaves leached for five days. At the end of the leaching period the calcium concentration was essentially the same as at the beginning. The actual concentration was essentially the same as at the beginning. The actual concentration was slightly increased in some leaves because organic losses due to leaching were greater than calcium losses.

Cromack's leaves ranged from .07 to .9 percent magnesium ($\bar{x}$=.2%). The average concentration of magnesium in alder leaves was .1 percent.

No data were available on leaching of pine needles or old field litter so deciduous values were used. Concentrations of nutrients in unleached litter were taken from Cromack for pine needles and from data collected by Coweeta personnel for old field litter.

Concentrations of nutrients in detritus are presented in Table 20. In the old field stream, detritus was primarily grasses. The average potassium concentration in old field litter was about .9 percent (Table 20). Calcium and magnesium concentrations were .5 and .2 percent respectively in unleached litter. A value of .1 percent potassium was chosen for all detritus (leached litter in the stream). Since little leaching of calcium and magnesium occurred, the .5 and .2 percent figures were used for detritus.

Detritus in the hardwood stream was mainly deciduous leaves and Rhododendron. The nutrient content of detritus was .1 percent potassium, 1 percent calcium and .2 percent magnesium based on the analyses described above. The same values were used for coppice detritus which was similar to hardwood detritus except that it had fewer Rhododendron leaves. Pine litter was .2 percent potassium, .66 percent calcium and .1 percent magnesium (Cromack 1972). Detritus was calculated to be .1 percent potassium, .66 percent calcium and .1 percent magnesium. Littoral shrubs contributed about 20 percent of the detritus in this stream but this did not significantly change the concentrations of nutrients.

The product of the mass of detritus and the percent composition of nutrients yielded the standing crop of nutrients in the detritus of each stream. Seasonal standing crops (mg/m_2) for calcium, potassium and magnesium for detritus and each trophic level are presented in Appen. Tables 2-4.

Most calcium in the consumers was tied up in the detritivore compartment by crayfish, which concentrate calcium in their exoskeletons. In several instances there was more calcium in the standing crop of detritivores than in the standing crop of detritus Appen. (Table 2). Salamanders were also important concentrators of calcium as was shown by the large standing crops of calcium in the predator compartment. These data are analogous to forest floor decomposer populations where a high percentage of primary consumers are Diplopoda. Reichle et al. (1969) suggested that in these systems the consumer trophic level represents a sink in the food chain distribution of calcium. Based on the present study, it is suggested that since crayfish and salamanders have a longer life span than other benthic organisms, and since very little calcium is leached from leaves prior to their consumption, these animals form a calcium sink, not only within the food chain, but in the entire remineralization process. With the exception of two instances when crayfish were absent, insects were responsible for less than 10 percent of the calcium in the consumer compartments. In nine of sixteen data sets in Appen. Table 3, insects were responsible for over half of the standing crop of potassium in the predator compartment. This emphasizes the importance of potassium in insects.

Table 20. Concentrations of nutrients in various types of stream detritus and ground litter, reported as percents.

		Old field	Hardwood	Pine	Coppice
Calcium	litter	.53	1.0	.66	1.0
	detritus	.53	1.0	.66	1.0
Potassium	litter	.9	.5	.2	.5
	detritus	.1	.1	.1	.1
Magnesium	litter	.2	.2	.1	.2
	detritus	.2	.2	.1	.2

The columns marked I in Appen. Table 6 show an increase in potassium concentration with an increase in trophic level. The columns marked i show a trend toward an increase in potassium with increasing trophic level but one point does not agree. Total detritivores should be compared with total predators and insect detritivores with insect predators. Grazers should also be compared with insect predators. These data support the trophic level increase of potassium observed by Hasanen and Miettinen (1963) who found a three fold increase in 137Cs (a potassium analog) in piscivorous blue gills when compared to their insectivorous prey. They did not compare the prey organisms with their food.

In a terrestrial study, Van Hook (1971) found a decrease in potassium concentration from the primary producer level (14.28 mg/g) to the herbivore level (1.87 mg/g) but the vegetation in that study had over an order of magnitude more potassium than Coweeta detritus (1.0 mg/g).

Although the amount of magnesium in the detritus compartments was about twice the amount of potassium, the standing crops of magnesium and potassium in consumer trophic levels were similar. There were four data sets in Appen. Table 4 in which the amount of magnesium in the insect detritivores exceeded the amount in crayfish alone, i.e. the insect portion of the detritivores comprised more than half of the compartment. These were the hardwood stream in fall and spring, the pine stream in fall and the coppice stream in spring. The salamanders contributed most of the magnesium to the predator compartment. Grazers represented a very small portion of magnesium in the total standing crop of consumers.

A decrease in magnesium concentrations was associated with an increase in trophic levels (Appen. Table 7). The relationship can best be seen by comparing total detritivores with total predators, insect detritivores with insect predators, or grazers with insect predators, or grazers with insect predators. The relationship breaks down when herbivorous insects are compared to total predators. The data sets marked D (Appen. Table 7) illustrate the relationship best and those marked d have one point which does not fit the trend.

Trophic Level Nutrient Concentration

The trophic level nutrient concentrations (Appen. Tables 5, 6, 7) were obtained by dividing the standing crops of nutrients (Appen. Table 2-4) by the standing crop biomass (Table 19). The data sets marked D show a decrease in calcium concentration with increase in trophic level or more specifically a decrease from the total in detritivores to total in the predators. These data mainly reflect the calcium concentrations in the crayfish and salamanders. A more interesting comparison is the decrease in calcium concentration in the detritus : insect detritivore : insect predator relationship. It is interesting to note that grazers frequently had higher calcium concentrations than detritivores. Diatoms were the most frequent algae observed in grazer diets and Vollenweider (1950) has shown that high calcium concentrations were needed by some diatoms.

Like calcium, most potassium in the consumers was tied up in the detritivore compartment by the crayfish. This was because of their size rather than the concentration of potassium in the organism. The amount of potassium in consumer and detritus compartments (Appen. Table 3) was about an order of magnitude less than the amount of calcium (Appen. Table 2). There was less potassium than calcium in the detritivore compartment because crayfish do not accumulate potassium as they do calcium. There were no occasions when the standing crop of potassium in detritivores exceeded that of detritus. Insect detritivores showed a two to eight fold increase in potassium concentration over the detritus compartment (Appen. Table 6) and the total detritivore compartment showed at least a two fold increase.

SECTION XI

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SECTION XII

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SECTION XIII

PUBLICATIONS RESULTING FROM STUDY

1. Woodall, W. R. 1969. A Comparison of Aquatic Insects in Four Different Watersheds. M. S. Thesis. Univ. of Ga. 111 p.

2. Wallace, J. B., W. R. Woodall, and F. F. Sherberger. 1970. Breakdown of leaves by feeding of *Peltoperla maria* nymphs. Ann. Ent. Soc. Amer. 63: 562-67.

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*Note - formal publications are in progress from the above two theses.

SECTION XIV

APPENDICES

Tables

1. Number of individuals per m^2.
2. Seasonal standing crops of calcium (mg/m^2) for each trophic level.
3. Seasonal standing crops of potassium (mg/m^2) for each trophic level.
4. Seasonal standing crops of magnesium (mg/m^2) for each trophic level.
5. Trophic level concentrations of calcium (mg/gm) determined by dividing the standing crop of cations by the standing crop of biomass.
6. Trophic level concentrations of potassium (mg/gm) determined by dividing the standing crop of cations by the standing crop of biomass.
7. Trophic level concentrations of magnesium (in mg/gm) determined by dividing the standing crop of cations by the standing crop of biomass.

Appen. Table 1. Number of individuals per m^2. Seasonal values are monthly averages. Summer (S), Fall (F), Winter (W), Spring (Sp)

Taxon	Season	Old field	Hardwood	Pine	Coppice
Cambarus	S	11.7	3.7	6.3	4.3
	F	0	2.5	5	0
	W	5	2.7	5	5.3
	Sp	7.3	2.7	4	2.3
Ephemerella	S	9.3	0	5	15.3
	F	4	0	1.5	12.5
	W	13.3	21.7	25	41.7
	Sp	234.3	15.3	128.3	76
Stenonema	S	10	24	19.3	12
	F	8	54	13	16
	W	8.3	37	16	12.3
	Sp	8	38	24.7	12.7
Paraleptophlebia	S	2	53	6.3	4.3
	F	0	89	26.5	25
	W	30.7	72	15	48.7
	Sp	54.3	154.7	53.3	11.3
Lanthus	S	7.5	3	8	8.3
	F	2.5	5.5	6	0
	W	3	4.3	12.3	10.3
	Sp	10	1.3	17	2.7

Appen. Table 1 (Continued).

Taxon	Season	Old field	Hardwood	Pine	Coppice
Peltoperla	S	3	57	101.8	35
	F	3	148	70	158
	W	4	161.7	100.3	308
	Sp	4.3	234.3	17	79
Isogenus	S	0	19.8	27.3	20.3
	F	20	35	28	54
	W	3.7	11.7	4	51.3
	Sp	17.3	10.3	23	33
Elmidae (Adult)	S	33.7	44.3	44.3	7
	F	232.5	5.5	25	16.5
	W	129.7	16.3	29	10.3
	Sp	191.3	64.3	125.3	17.3
Elmidae (Larvae)	S	133	11	78	15.3
	F	223.5	4.7	27.5	0
	W	78	6.3	32.7	2.7
	Sp	241	1	104.7	16.7
Rhyacophila	S	7	11.7	4.3	10
	F	35	11.5	23.5	21.5
	W	31.7	22.7	16	34.7
	Sp	20.3	20	6	16.7

Appen. Table 1 (Continued)

Taxon	Season	Old field	Hardwood	Pine	Coppice
Diplectrona	S	36.3	73.7	23.3	33
	F	88.5	116	24.5	186.5
	W	110	116.3	25.3	111.3
	Sp	145.3	57	24	30
Parapsyche	S	5.3	3.3	10	26.7
	F	28.5	13	13.5	2
	W	6.7	7	46	30
	Sp	10	7	5.7	5.7
Chironomidae	S	183.7	120	90.7	81.6
	F	37.5	61	87	136
	W	300	60	29.3	151.7
	Sp	319	123.3	59.3	76.7
Tipula	S	10	1	1	1
	F	16	0	5.5	48.5
	W	8.3	4.7	1.3	52.3
	Sp	1.7	8.7	6	2.3
Eriocera	S	5	26.7	7	31.3
	F	13.5	53.5	28.5	39.5
	W	153.6	63	23.6	46.7
	Sp	131	69	26.3	43

Appen. Table 1 (Continued)

Taxon	Season	Old field	Hardwood	Pine	Coppice
Desmognathus	S	1	3.7	4.7	4.7
	F	8	2.5	11	5.5
	W	4.7	4.3	3	11.3
	Sp	5	5.3	2.3	1

Appen. Table 2. Seasonal standing crops of calcium (mg/m^2) for each trophic level. Values are means of monthly samples. * = detritivores without crayfish; ** = predators without salamanders.

Watershed	Trophic level	Summer	Fall	Winter	Spring
Old field	Detritus	180	180	730	420
	Detritivores	852.51	1.41	571.31	155.23
	Detritivores*	4.59	1.41	2.10	4.08
	Grazers	.26	.23	.4	1.06
	Predators	4.13	20.37	21.47	13.24
	Predators**	.32	.58	.64	1.67
Hardwood	Detritus	550	1530	1460	1020
	Detritivores	270.64	16.25	311.18	62.76
	Detritivores*	2.49	2.84	3.81	7.03
	Grazers	.25	.29	.27	.34
	Predators	14.66	6.84	19.53	13.35
	Predators**	.56	.66	.48	1.09
Pine	Detritus	430	470	440	530
	Detritivores	458.73	28.17	605.38	87.46
	Detritivores*	2.16	1.34	2.03	4.89
	Grazers	.13	.14	.26	.37
	Predators	18.56	27.79	13.92	6.92
	Predators**	.54	.58	.63	1.6
Coppice	Detritus	510	2160	1580	490
	Detritivores	313.26	3.92	614.99	50.07
	Detritivores*	1.63	3.92	11.64	2.59
	Grazers	.31	.31	.36	.34
	Predators	18.76	14.61	51.4	4.16
	Predators**	.84	1.01	1.33	1.85

Appen. Table 3. Seasonal standing crops of potassium (mg/m^2) for each trophic level. Values are means of monthly samples. * = detritivores without crayfish; ** = predators without salamanders.

Watershed	Trophic level	Summer	Fall	Winter	Spring
Old field	Detritus	34	34	137	80
	Detritivores	22.79	1.35	12.97	8.94
	Detritivores*	6.73	1.35	2.19	6.08
	Grazers	.1	.16	.42	1.95
	Predators	1.66	1.6	2.17	2.53
	Predators**	1.44	.44	.95	1.85
Hardwood	Detritus	55	153	146	102
	Detritivores	6.9	1.67	8.15	6.49
	Detritivores*	1.82	1.44	2.43	5.43
	Grazers	.25	.24	.28	.34
	Predators	1.52	.97	1.73	1.88
	Predators**	.69	.61	.28	1.16
Pine	Detritus	65	71	67	80
	Detritivores	10.2	1.41	12.63	5.16
	Detritivores*	1.55	.91	1.2	3.59
	Grazers	.1	.11	.15	.21
	Predators	1.87	2.1	1.58	2.12
	Predators**	.82	.51	.8	1.81
Coppice	Detritus	51	216	158	49
	Detritivores	7.37	3.91	21.66	2.87
	Detritivores*	1.47	3.91	10.23	1.96
	Grazers	.27	.25	.26	.25
	Predators	2.17	1.62	4.85	1.34
	Predators**	1.12	.82	1.92	1.21

Appen. Table 4. Seasonal standing crops of magnesium (mg/m^2) for each trophic level. Values are means of monthly samples. * = detritivores without crayfish; ** = predators without salamanders.

Watershed	Trophic level	Summer	Fall	Winter	Spring
Old field	Detritus	68	68	274	160
	Detritivores	21.83	.64	14.06	5.35
	Detritivores*	2.39	.65	1.01	1.89
	Grazers	.06	.08	.2	.45
	Predators	.86	1.31	1.48	1.35
	Predators**	.65	.2	.31	.7
Hardwood	Detritus	110	306	292	204
	Detritivores	7.34	1.66	8.84	4.66
	Detritivores*	1.19	1.35	1.79	3.83
	Grazers	.11	.11	.11	.15
	Predators	1.04	.61	1.28	1.14
	Predators**	.25	.26	.21	.45
Pine	Detritus	65	71	67	80
	Detritivores	11.48	1.43	14.76	3.15
	Detritivores*	1.01	.82	.92	1.25
	Grazers	.05	.06	.11	.15
	Predators	1.28	1.75	1.02	.99
	Predators**	.28	.13	.27	.69
Coppice	Detritus	102	432	316	98
	Detritivores	7.92	1.88	19.64	2.39
	Detritivores*	.78	1.88	5.81	1.3
	Grazers	.13	.13	.12	.14
	Predators	1.4	1.14	3.5	.77
	Predators	.4	.38	.69	.64

Appen. Table 5. Trophic level concentrations of calcium (mg/gm) determined by dividing the standing crop of cations by the standing crop of biomass. * = detritivores without crayfish; ** = predators without salamanders; D = decrease in trophic level concentrations for that data set.

Watershed	Trophic level	Summer	Fall	Winter	Spring
Old field	Detritus	5.3 D	5.3 D	5.3 D	5.3 D
	Detritivores	89.4	3.9	92.8	68.2
	Detritivores*	4.2	3.9	4.3	5.3
	Grazers	7.4	3.7	4.2	5.3
	Predators	11.9	31.0	30.6	16.2
	Predators**	1.2	3.8	3.7	3.2
Hardwood	Detritus	10.0 D	10.0 D	10.0 D	10.0 D
	Detritivores	82.7	19.4	77.5	27.7
	Detritivores*	4.1	4.0	4.0	4.1
	Grazers	4.0	4.4	4.1	4.5
	Predators	28.3	19.5	31.3	22.6
	Predators**	3.5	3.4	3.4	3.9
Pine	Detritus	6.6 D	6.6 D	6.6 D	6.6 D
	Detritivores	90.0	46.9	92.3	44.4
	Detritivores*	3.9	4.0	3.7	4.2
	Grazers	4.0	2.4	4.4	5.9
	Predators	27.7	32.2	25.4	11.0
	Predators**	2.5	3.4	3.0	3.2
Coppice	Detritus	10.0 D	10.0	10.0 D	10.0 D
	Detritivores	88.9	3.4	71.6	43.5
	Detritivores*	3.9	3.4	4.5	3.8
	Grazers	4.0	3.9	4.1	5.3
	Predators	25.0	24.7	30.1	7.6
	Predators**	3.0	4.1	3.1	3.8

Appen. Table 6. Trophic level concentrations of potassium (mg/gm) determined by dividing the standing crop of cations by the standing crop of biomass. * = detritivores without crayfish; ** = predators without salamanders; I = increase in concentration for that data set; i = some trend toward increase for that data set.

Watershed	Trophic level	Summer	Fall	Winter	Spring
Old field	Detritus	1.0 i	1.0	1.0 I	1.0
	Detritivores	2.3	3.7	2.1	3.9
	Detritivores*	6.2	3.7	4.5	7.9
	Grazers	2.8	2.6	4.5	9.7
	Predators	4.8	2.4	3.0	3.1
	Predators**	5.8	2.8	5.5	3.5
Hardwood	Detritus	1.0 I	1.0 i	1.0	1.0 I
	Detritivores	2.1	2.0	2.0	2.8
	Detritivores*	3.0	2.0	2.5	3.1
	Grazers	4.0	3.6	4.4	4.5
	Predators	2.9	2.7	2.7	3.1
	Predators**	4.3	3.1	2.0	4.1
Pine	Detritus	1.0 I	1.0 i	1.0 I	1.0 I
	Detritivores	2.0	2.3	2.0	2.6
	Detritivores*	2.8	2.7	2.2	3.1
	Grazers	3.6	3.4	2.6	3.3
	Predators	2.9	2.7	2.7	3.1
	Predators**	3.7	3.0	3.8	3.7
Coppice	Detritus	1.0 I	1.0 i	1.0 I	1.0
	Detritivores	2.0	3.4	2.5	2.4
	Detritivores*	3.5	3.4	3.9	2.9
	Grazers	3.4	3.2	2.9	3.9
	Predators	2.9	2.7	2.8	2.4
	Predators**	4.1	3.7	5.0	2.7

Appen. Table 7. Trophic level concentrations of magnesium (in mg/gm) determined by dividing the standing crop of cations by the standing crop of biomass. * = detritivores without crayfish; ** = predators without salamanders; D = decrease in trophic level concentration in that data set; d = trend for decrease in that data set.

Watershed	Trophic level	Summer	Fall	Winter	Spring
Old field	Detritus	2.0	2.0 d	2.0 D	2.0 D
	Detritivores	2.2	1.7	2.3	2.3
	Detritivores*	2.2	1.7	2.1	2.4
	Grazers	1.8	1.3	2.1	2.2
	Predators	2.5	1.9	2.1	1.6
	Predators**	2.6	1.3	1.8	1.3
Hardwood	Detritus	2.0 D	2.0 D	2.0 D	2.0 D
	Detritivores	2.2	1.9	2.2	2.0
	Detritivores*	1.9	1.9	1.8	2.2
	Grazers	1.7	1.6	1.6	1.9
	Predators	2.0	1.7	2.0	1.9
	Predators**	1.5	1.3	1.5	1.6
Pine	Detritus	1.0 D	1.0 D	1.0 D	1.0
	Detritivores	2.2	2.3	2.2	1.5
	Detritivores*	1.8	2.4	1.7	1.1
	Grazers	1.6	2.3	1.8	2.4
	Predators	1.9	2.0	1.8	1.5
	Predators**	1.3	0.7	1.2	1.4
Coppice	Detritus	2.0 D	2.0 d	2.0 d	2.0 D
	Detritivores	2.0	1.6	2.0	2.0
	Detritivores*	1.8	1.6	2.2	1.9
	Grazers	1.7	1.6	1.4	2.2
	Predators	1.9	1.9	2.0	1.4
	Predators**	1.4	1.5	1.6	1.3